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16

Aeration in Aquaria

A. L. Downing & G. A. Truesdale

Water Pollution Research Laboratory, Stevenage, Herts., England

(Text-figures 1-5)

Introduction

It is well known that to keep fish alive and healthy in aquaria it is necessary to ensure that the water contains an adequate concentration of dissolved oxygen. This can usually be arranged without a detailed knowledge of the physical and biochemical processes governing the level of dissolved oxygen attained under given conditions. In some cases when, for instance, there are few fish in a large volume of water with a large exposed surface and containing perhaps a few green plants, there is no apparent need to provide additional aeration. In other cases all that may be required is a stream of air bubbles passed through the water. In current research on the development of tests for the toxicity of effluents to be discharged into surface waters, however, it is sometimes desirable not merely to keep fish adequately supplied with oxygen, but also, since the toxicity of certain poisons is known to depend on the level of dissolved oxygen (Downing, 1954), to keep this concentration within prescribed limits without at the same time causing undue loss of volatile constituents. This demands a more detailed knowledge of the aeration process and of the other factors affecting the concentration of dissolved oxygen.

Factors Affecting the Concentration of Dissolved Oxygen

The concentration of dissolved oxygen is determined by the relative magnitudes of the rates of supply and demand. On the one hand oxygen is consumed by the respiration of fish and plants, if these are present, and possibly, to a much lesser extent, by the bio-oxidation of metabolic products; on the other it is re-supplied to the water by absorption from the atmosphere and by the photosynthetic activity of plants. The assumption of Breder (1931) that photosynthesis has little influence on the concentration of dissolved oxygen cannot be accepted as an accurate generalization, although it is true that in many cases its role may be unimportant. The difficulty is that its influence cannot often be calculated quantitatively because of an inadequate knowledge of the rates of consumption or evolution of oxygen by fish or plants under given conditions. Nevertheless approximate average values of these rates for certain fishes and plants are known, and they may be used when applicable to predict the variation of dissolved oxygen in an aquarium. Before this can be done, however, the rate of absorption of oxygen from the air must be measured or estimated.

Absorption of Atmospheric Oxygen by Water

In quiescent conditions oxygen penetrates into water by molecular diffusion in accordance with Fick's law. In moving water this process is augmented by turbulent mixing of the surface layers with the main body of the liquid and by the creation of fresh surfaces. It is proposed to consider the aeration of aquaria in which the general level of turbulence, created by the devices used to promote aeration, by the movement of fish, and by miscellaneous minor disturbances is sufficient to maintain a sensibly uniform concentration of dissolved oxygen at all points below the outermost surface layers, which are assumed to be saturated with oxygen. It seems very probable that this condition will be approximately satisfied in most small aquaria (not deeper than, say, about 1 metre) since experience shows that, unless special precautions are taken to control vibrations and the temperature and humidity of the air above the surface, gradients in the oxygen concentration

are not detectable even in apparently stagnant water. This is largely due to "streaming" resulting from density changes caused by cooling of the surface layers by evaporation. In very large aquaria in which aeration was promoted by a stream of bubbles liberated a long way from the center of the bottom of the tank, such conditions might not apply. In this case, however, the rate of change of oxygen concentration at any point would be governed by random movement of the fish and any other incidental disturbances; since this would be largely unpredictable it will not be considered further.

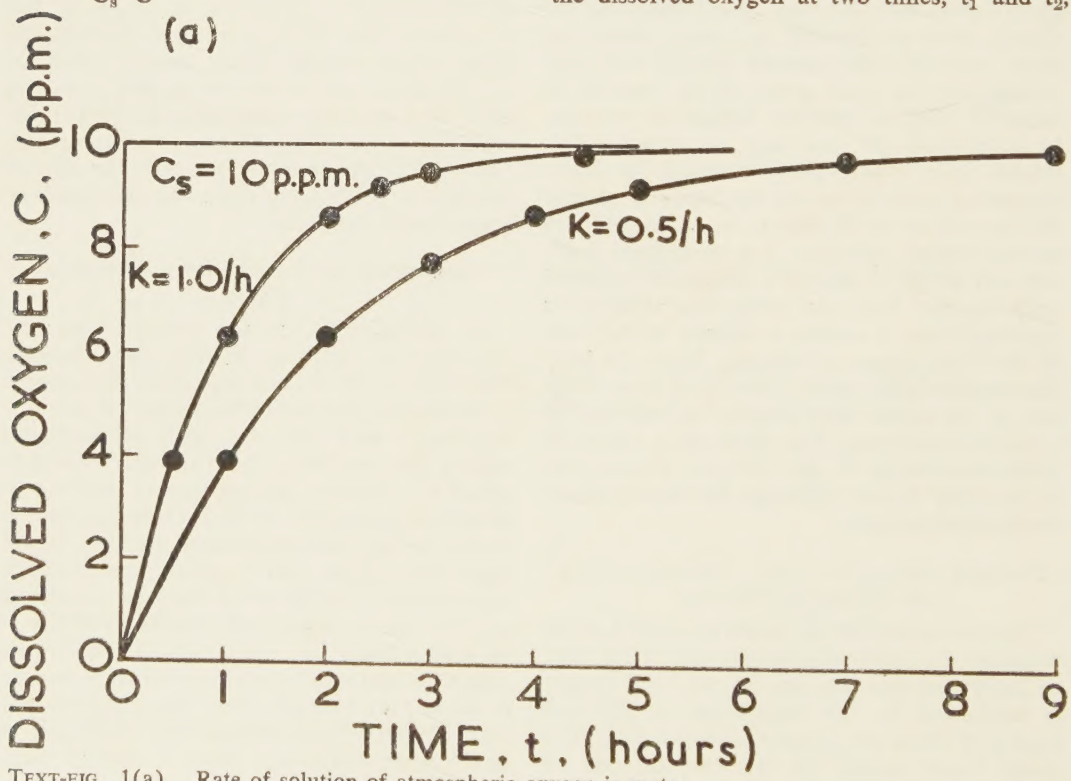
For aquaria in which there is reasonably uniform mixing it is found that the rate of change of dissolved oxygen at any time, t, is directly proportional to the difference between the saturation concentration, C_s, and the concentration, C, in the water (Lewis & Whitman, 1924). That is,

$$\frac{dC}{dt} = K\,(C_s - C) \quad \text{.....(1)}$$

and, integrating,

$$\log_e \frac{C_s}{C_s - C} = Kt \quad \text{.....(2)},$$

where K, the over-all absorption coefficient, measures the rate of change of concentration of dissolved oxygen when the saturation deficit, $C_s - C$, is unity. K has dimensions T^{-1} and is generally expressed in reciprocal hours. Thus the increase of dissolved oxygen with time, due to aeration, follows an exponential curve, the exact form of which depends on the magnitude of the absorption coefficient (Text-fig. 1a). There is however no simple method for predicting accurately the magnitude of K from a knowledge of the physical characteristics of the system; such theories as there are demand a knowledge of hypothetical or difficultly measurable quantities such as the thickness of the stagnant film at the water surface (Lewis & Whitman, 1924), the time of exposure of freshly created surfaces (Higbie, 1935; Pasveer, 1953), or the rate of mixing of the water (Phelps, 1947). Fortunately, however, if it is assumed that the effect on the rate of aeration due to the movement of fish is negligible, as will generally be the case except perhaps in stagnant water, then the rate of aeration can be measured directly in the aquarium in their absence. This is conveniently done by measuring the dissolved oxygen at two times, t_1 and t_2,



TEXT-FIG. 1(a). Rate of solution of atmospheric oxygen in water.
Temperature 13.90° C.
Solubility of oxygen, C_s, from moist air = 10 p.p.m.
Equation of absorption curves: $\log_e \frac{C_s}{C_s - C} = Kt$.

after partial deoxygenation of the water, followed by substitution of the values in an equation, derived from Equation (1), of the form

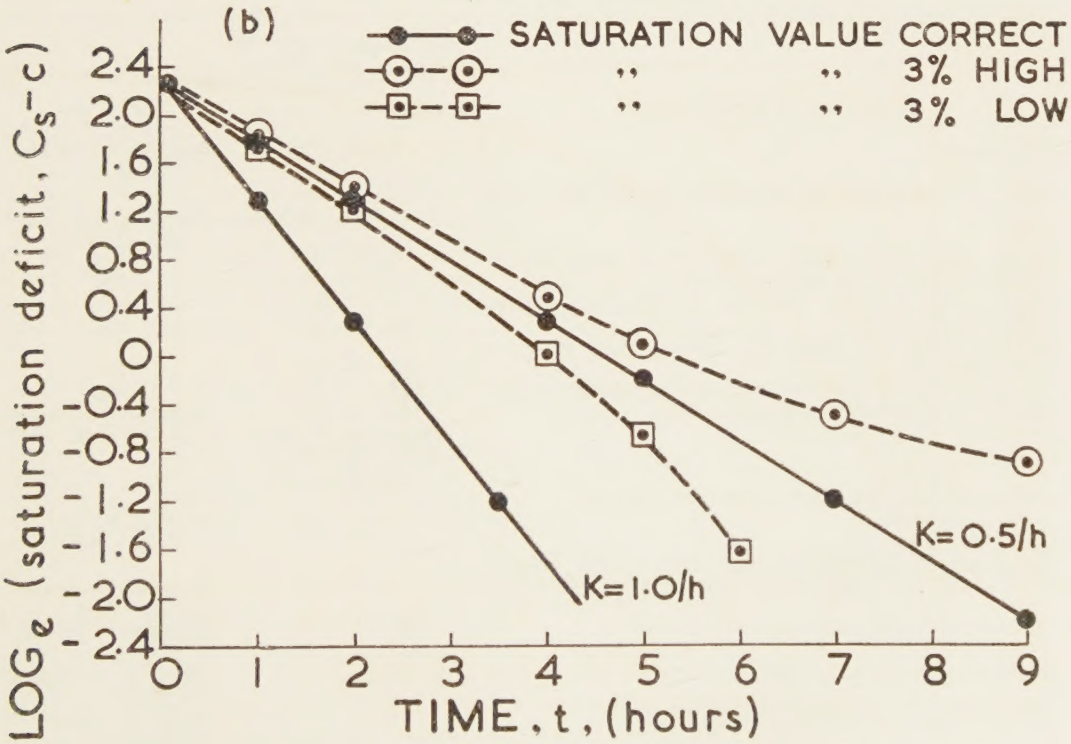
$$\log_e \frac{C_s - C_1}{C_s - C_2} = K(t_2 - t_1) \quad \ldots\ldots (3),$$

where C_1 and C_2 are the oxygen concentrations at t_1 and t_2. Alternatively K may be evaluated from the slope of the straight line obtained by plotting the logarithm of periodic observations of the saturation deficit against time. The importance of having an accurate knowledge of the solubility (Truesdale, Downing & Lowden, 1955) for these computations is demonstrated in Text-fig. 1b.

The value of K obtained in the manner indicated does however depend on the volume of water, V, and the area of the exposed surface, A, the ratio V/A being sometimes referred to as the "aeration depth." In considering the range of values in which the rate of aeration may vary under different conditions, it is therefore convenient to use a transfer coefficient, f, (sometimes called the "exit coefficient," (Gameson, Truesdale & Downing, 1955)) defined by the relation

$$K = \frac{f.A}{V}, \quad \ldots\ldots (4)$$

which measures the rate of change of dissolved oxygen in a unit depth of water when the saturation deficit is unity. It has dimensions LT^{-1} and is usually expressed in cm./h. It is also equivalent to the amount of oxygen passing through unit area of surface in unit time when the deficit is unity, 1cm./h. being equivalent to 1μg./cm.^{2}, p.p.m., h. For a system having f = 10cm./h. and an aeration depth 10 cm., the over-all absorption coefficient would be 1.0/h. so that the rate of solution when the deficit was 10 p.p.m. would be 10 p.p.m./h. In making predictions of this kind it is of course tacitly assumed that the mass transfer coefficient is unaffected by changes in the aeration depth provided there is no obvious difference in the conditions of agitation at the surface from those for which the coefficient was measured. This is generally only approximately true for limited changes in V/A, and if an accurate knowledge of the rate of aeration in a particular system is required it is much safer to determine this directly in the manner indicated. The published values of mass-transfer coefficients for different aeration systems show that they are extremely dependent on the degree and type of agitation in the water and may vary between values of less than 1.0 cm./h. for stagnant water to values



TEXT-FIG. 1(b). Linear variation of the logarithm of the saturation deficit with time; effect of incorrect saturation values.

of the order of 500 cm./h. for rapidly stirred water (Table 1).

The mass-transfer coefficient is also dependent on the temperature, the concentration of dissolved salts, and the condition of the surface. For instance, in the temperature range 0 to 35° C., f increases by between 2.2 and 2.3 per cent. of the value at 20° C. per degree Centigrade increase in temperature (Downing & Truesdale, 1955). On the other hand it appears to be reduced by dissolved salts since the rate of solution in pure sea water and in sodium chloride solution of the same salinity is lower than that in pure water under the same conditions (Department of Scientific and Industrial Research, 1956). Soluble or insoluble surface contaminants or surface-active agents also generally cause a decrease in the rate of solution although the magnitude depends very much on their concentration and the conditions of agitation (Downing & Truesdale, 1955).

Prediction of Dissolved Oxygen Concentrations in Aquaria

Given a knowledge of the rate of absorption of oxygen from the air and the rate of absorption or production of oxygen by respiration or photosynthesis, we are in a position to make approximate calculations of the variation of dissolved oxygen concentration with time. To simplify matters we may assume that fish and plants consume oxygen at a constant rate K_1 p.p.m./h. and K_2 p.p.m./h. respectively, and that during daylight oxygen is produced by photosynthesis at a constant rate K_3 p.p.m./h.

The rate of change of concentration of dissolved oxygen is given by

$$\frac{dC}{dt} = K(C_s - C) - K_1 - K_2 + K_3 \quad \ldots (5)$$

and

$$\log_e \left\{ \frac{K(C_s - C_o) - K_1 - K_2 + K_3}{K(C_s - C) - K_1 - K_2 + K_3} \right\} = Kt \quad \ldots (6),$$

so that

$$C = e^{-Kt} C_o + \frac{(1 - e^{-Kt})\,(KC_s - K_1 - K_2 + K_3)}{K} \quad \ldots (7),$$

where K is the over-all absorption coefficient and C_o is the initial concentration of dissolved oxygen.

Table 1. Observed Values of the Mass-Transfer Coefficient, f, for Oxygen in Stagnant and Agitated Water

Description of aeration system	Approximate value or range of values taken by mass-transfer coefficient, f. (cm./h.)	Reference
Stagnant water	0.2 — 0.5	Holroyd & Parker (1952)
Slowly stirred water: no appreciable disturbance of the surface	1.0 — 5.0	Downing & Truesdale (1955)
Slowly stirred water: slight disturbance at the surface	1.0 — 10	do.
Rapidly stirred water: regular vortices at the surface	10 — 50	do.
Rapidly stirred water: irregular vortices and severely disturbed surface	*50 — 500	do.
Regular progressive waves (2.8-10.2 cm. high) in shallow water	*10 — 37	do.
"Choppy" waves (6.4-13.3 cm. high) in shallow water	*11 — 25	do.
Shallow and turbulent Lakeland beck	*30 — 200 (Depending on flow, depth, and roughness of bed)	Gameson, Truesdale & Downing (1955)
"Model Stream" flowing in channels, velocity 0.6-15 m./min.	1 — 30	Streeter, Wright & Kehr (1936)
Water surface ruffled by tangential air stream, velocity, measured near the surface, increasing to 13.5 m./sec.	1.5 — 63	Downing & Truesdale (1955)
Diffused air bubbles, 1-5 mm. in diameter	180	Holroyd & Parker (1952)
Diffused air bubbles, 2.4 mm. in diameter	Ca. 90	Scouller & Watson (1934)
Diffused oxygen bubbles, 2 mm. in diameter	96	Ippen & Carver (1954)

*Nominal values calculated using an aeration depth determined from the volume of water and the area of the undisturbed surface.

The use of this equation may be illustrated by inserting in it some typical values of the variable quantities.

Consider first the case in which no plants are present in the aquarium so that K_2 and K_3 are zero; suppose that the volume of fresh water is 100 litres with an exposed surface of 5,000 sq.cm., that this contains 10 brook trout each weighing 25 gm. and consuming oxygen at a rate of 100 ml. oxygen/Kg. fish, h., a reasonably approximate figure (Graham, 1949). Suppose further that the temperature is 13.9° C. and that the barometric pressure is 760 mm. Hg, so that the solubility of oxygen is 10 p.p.m. (Truesdale, Downing & Lowden, 1955). If no additional aeration is provided the mass transfer coefficient for the entry of oxygen through the surface will be approximately 1.0 cm./h. (Table 1). Thus

$$K = \frac{5 \times 10^3}{10^2 \times 10^3} = 0.05/\text{h}.$$

and

$$K_1 = \frac{10 \times 25}{1000} \times 100 \times 1.43 \times \frac{1}{100} = 0.36 \text{ p.p.m./h.}$$

The oxygen concentration will therefore tend to an equilibrium value given from Equation 5 when

$$\frac{dC}{dt} = 0,$$

such that

$$0.05(10-C) = 0.36$$
$$C = 2.8 \text{ p.p.m.},$$

which is approaching a dangerously low level for trout. In theory the equilibrium concentration will be reached only after an infinite time, but if the water is initially saturated with oxygen it can be shown, by substitution in Equation (5), that a concentration within about 0.1 p.p.m. of the equilibrium value will be reached after time, t, given from Equation (6) by

$$t = \frac{1}{0.05} \log_e \left(\frac{-0.36}{(0.05)\ (7.1) - 0.36} \right)$$
$$= 85.5 \text{ hours}$$

and that the variation of dissolved oxygen with time will follow curve AB (Text-fig. 2). Thus even in the short space of a day, the oxygen concentration would be lowered to half its initial value.

Validity of the Theoretical Relations

At present there is little or no evidence to support the validity of the hypothetical conclusions deduced from Equations (5), (6) and (7). Some preliminary experimental studies with rainbow trout do, however, indicate that approximately correct predictions of the average concentration of dissolved oxygen in an aquarium can be made in this way (Alabaster, 1956). It is found that the oxygen concentration at any instant fluctuates about the average value between quite wide limits. This is presumably due to variations in both the rate of solution of oxygen and the oxygen consumption of the fish. If the approximate variability in these two quantities is known we can determine the probable variation in the dissolved oxygen. Thus suppose that the random variations of K and K_1 about their mean values are represented by standard errors aK, and bK_1, then the variation in the equilibrium concentration of dissolved oxygen for an aquarium containing only fish may be expressed as the standard error, σ, in the quotient K_1/K in the equation $C = C_s - K_1/K$, derived from (5), i.e., by

$$\sigma = K_1/K \sqrt{(a^2 + b^2)}.$$

Thus the variation in the equilibrium dissolved oxygen concentration will increase as K decreases or as K_1 increases; that is, it will increase as the equilibrium concentration decreases.

For instance, in the case where $K = 0.05$, $K_1 = 0.36$, $a = b = 0.1$ and $C_s = 10$, we have

$$\sigma = 7.2 \sqrt{0.02}$$
$$= 1.02$$

Thus the mean equilibrium concentration and its standard error will be 2.8 and 1.02 p.p.m. For $K = 0.5$,

$$\sigma = 0.72 \sqrt{0.02}$$
$$= 0.1,$$

so that in this case the error in the equilibrium concentration, $C = 9.28$ p.p.m., will be only 0.1 p.p.m.

Adjustment of Conditions to Satisfy Oxygen Demands

The reduction of the oxygen concentration to a dangerously low level may be prevented by (i) reducing the population of fish, (ii) decreasing the aeration depth while keeping the volume constant, (iii) increasing the partial pressure of oxygen in the gas phase, (iv) changing the water at intervals or continuously, (v) increasing the rate of absorption of oxygen from the atmosphere, or (vi) making use of photosynthesis to produce oxygen. The first two possibilities (i) and (ii) are straightforward and will not be considered further.

Increasing the partial pressure of oxygen. (iii).

This will increase the saturation concentration of oxygen in the water, in accordance with Henry's law, so that for a given deficit, $C_s - C$, the concentration of dissolved oxygen will be greater.

Replacement of water. (iv).

If, as may sometimes be the case in toxicity tests, the volume of solution available for replacement is limited and we wish to maintain the oxygen concentration between prescribed limits, the minimum frequency of periodic replacement can be ascertained by substituting the appropriate values in Equation (6). Alternatively, the rate of change of oxygen concentration that would result from replacing the water in the aquarium continuously by water, saturated with oxygen, at a rate, v litres/h., assuming rapid and complete mixing, would be given by

$$dC/dt = v/V(C_s - C) \quad \text{.....(8)},$$

where V is the volume of the aquarium. Thus to maintain a given concentration, C, would require the water to be replaced at a rate given by

$$\frac{dC}{dt} = 0 = K(C_s - C) + \frac{v}{V}(C_s - C) - K_1 - K_2 + K_3 \quad \text{.....(9)}$$

so that

$$v = V\left[\frac{K_1 + K_2 - K_3}{(C_s - C)} - K\right] \quad \text{.....(10)}.$$

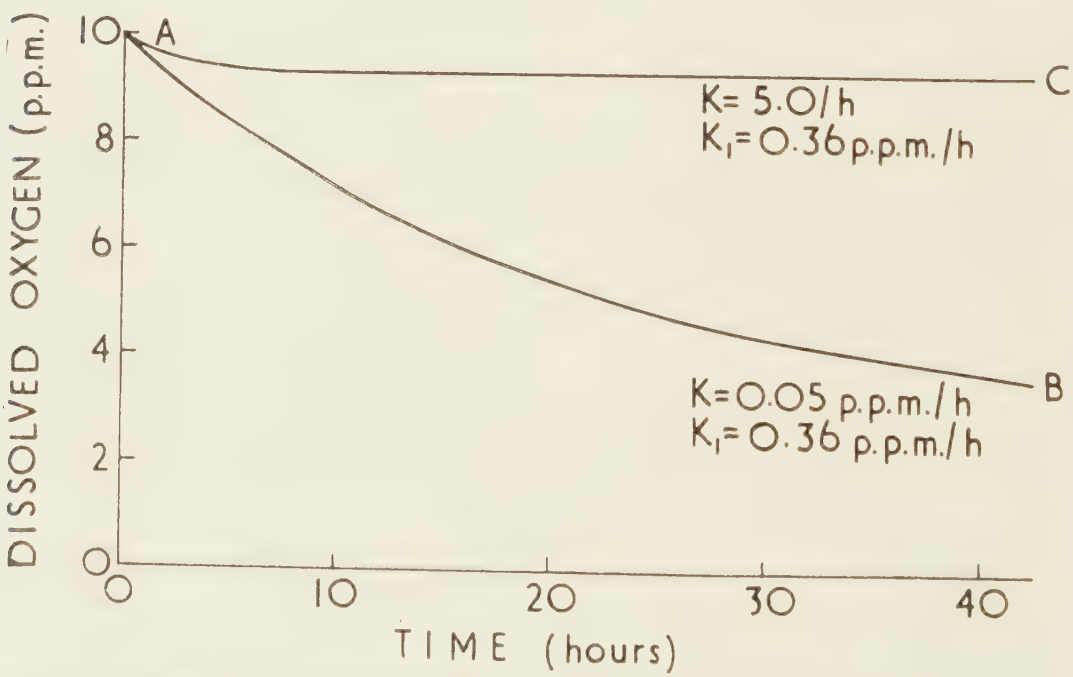
To maintain an equilibrium concentration C, of say 6 p.p.m., when $K_1 = 0.36$ p.p.m./h. and $K_2 = K_3 = 0$, would require a rate of replacement

$$v = 100\left(\frac{0.36}{4} - 0.05\right) = 4 \text{ l./h.}$$

These rates of replacement refer only to dissolved oxygen requirements, of course. In practice other factors such as the accumulation of noxious metabolic products might necessitate more frequent replacement.

Increasing the rate of aeration. (v).

If we prefer to increase the rate of aeration, then the minimum rate required to prevent the deficit, $C_s - C$, exceeding a given value D is given by $KD = 0.36$, ($K_2 = K_3 = 0$). For instance, if the previous equilibrium deficit is to be reduced from 7.2 p.p.m. to say 0.72 p.p.m., then K must be increased to 5.0/h. Once K had been increased to this value the variation of oxygen concentration with time would follow curve AC (Text-fig. 2). As already indicated, this rate of aeration could be obtained in several ways; in practice the most common and easiest method is to bubble air through the water. The approximate order of frequency of bubbles and rate of flow of air required may be determined using data published in the literature. For in-



TEXT-FIG. 2. Effect of the respiration of fish on the variation of concentration of dissolved oxygen in aquaria.

K: over-all absorption coefficient.

K_1: rate of consumption of dissolved oxygen by fish.

stance the average mass-transfer coefficient for streams of bubbles (from a porous diffuser) having an average radius of about 1 to 2 mm. has been found to be of the order of 200 cm./h. (Holroyd & Parker, 1949; Datta, Napier & Newitt, 1950), so that if we wish to increase K from 0.05 to 0.50, neglecting the effect of the bubbles on the aeration at the surface, the total surface area of the bubbles that must be present instantaneously is given from Equation (4) by

$$0.45 = \frac{200 \times A}{10^2 \times 10^3}.$$

$$\therefore \quad A = 225 \text{ sq. cm.}$$

Thus if we assume for this purpose that all the bubbles have a radius of 1 mm., the total number, N, that must be instantaneously present is $225/4\pi(0.1)^2$, that is, about 1,900. If the velocity of the bubbles is for simplicity assumed to be constant at the approximate terminal velocity for this size of bubble, 20 cm./sec. (Ippen & Carver, 1954), then the required frequency of production of bubbles, F, is given by

$$F = N \times \frac{\text{depth}}{\text{velocity}} = N \times 20/20, \text{ whence}$$

$$F = 1900 \text{ bubbles/sec.}$$

This corresponds to an airflow of about 475 ml./min.

In practice, it would be necessary to make preliminary trials with diffusers of different sizes and porosities to select one that gave bubbles of the size required, since the size is found to vary with porosity, loading, and the nature of the liquid.

It will of course be appreciated that this simple treatment neglects many factors such as the variation with depth of water of the bubble size and velocity as well as the partial pressure of oxygen within the bubble and hence of the saturation concentration of oxygen at the bubble interface. An interesting and more rigorous treatment of this subject is given by Pasveer (1954).

Production of oxygen by photosynthesis. (vi).

When living aquatic plants containing chlorophyll are illuminated, oxygen is produced by photosynthesis as a result of a complex series of reactions conventionally summarized by the equation

$$6\ CO_2 + 6\ H_2O + 675\ K \text{ cals} \rightarrow C_6H_{12}O_6 + 6\ O_2 \quad \text{.....(11)}$$

The energy absorbed is supplied by the light.

The mechanism of this process is extremely complicated and is by no means fully understood. For a given plant the rate of production of oxygen depends upon the conditions of illumination, the concentration of carbon dioxide and on other physical variables such as temperature and turbulence. It is also a function of many physiological factors responsible for varied and as yet unpredictable phenomena such as resting, fatigue, aging, inhibition, adaptation and the like. The difficulties encountered in studies of the kinetics of such a complex process in living organisms can hardly be exaggerated, and indeed doubts have often been expressed as to the possibility of deriving significant kinetic relationships. Nevertheless, at least for short periods, the rate of photosynthesis appears to remain constant in a constant environment, and it is proposed to illustrate the influence of the process on the balance of oxygen in an aquarium under such conditions.

With both the two main variables, light and carbon dioxide, a saturation level is reached above which increasing the intensity or concentration causes no change in the rate of photosynthesis, which is at a maximum with respect to these two factors. Measurements of maximum photosynthetic activity recorded in the literature relate to conditions in which at least by intention neither light nor carbon dioxide was limiting. We shall consider the effect due to an aquatic plant of tropical origins, *Valisneria spiralis* (commonly found in indoor aquaria in the United Kingdom and elsewhere), leaves of which, 30 cm. in length, were observed to produce 0.63 mg. oxygen per hour per leaf during daylight (Manning, Juday & Wolf, 1938). Assuming the leaves to be about 1 cm. wide, this rate of production is equal to about 2 mg. O_2/h., 100 cm.^{2}, which is within the range of values 1.3 — 7 mg. O_2/h., 100 cm.^{2} observed for other aquatic plants (Rabinowitch, 1951, p. 961).

In addition to producing oxygen when illuminated, the living plant is, of course, continuously respiring and for any given conditions the ratio of respiration to photosynthesis governs the level of oxygen in an aquarium. On the average the *rate* of respiration appears to be about 5-15 per cent. of photosynthesis, according to Rabinowitch (1951, p. 7) and Verduin (1952). For detailed information on photosynthesis the reader is referred to the standard text on the subject by Rabinowitch (1951).

Let us suppose the aquarium contains 70 leaves of *Valisneria spiralis,* producing oxygen at a constant rate of 0.63 mg. O_2/h., leaf during daylight and consuming oxygen by respiration at about 10 per cent. of this rate. Then $K_2 =$ 0.04 p.p.m./h. and $K_3 =$ 0.44 p.p.m./h. (The total volume of water is taken to be 100 litres, as before.)

Case I. If the rate of aeration was small (K = 0.05/h.) and the water was initially

saturated with oxygen, then with the aquarium always in darkness (*i.e.*, $K_3 = 0$), the dissolved oxygen would fall toward an equilibrium value of 2 p.p.m. (Equation 5) in accordance with curve ABHI (Text-fig. 3) which has been deduced from Equation (7).

Case II. If on the other hand, the aquarium was continuously illuminated and initially saturated with oxygen, it would become supersaturated, the concentration varying in accordance with curve AJ (Text-fig. 3), reaching an equilibrium value, C = 10.8 p.p.m., given from Equation (5) by

$$\frac{dC}{dt} = 0 = 0.05\ (10-C) - 0.36 - 0.04 + 0.44.$$

It should be noted that in this case an increase in the rate of aeration, K, to, say, 0.5/h., would reduce the degree of supersaturation to the equilibrium concentration C = 10.08 p.p.m. If the concentration of dissolved oxygen was initially less than the saturation value, then upon continuous illumination it would approach the equilibrium value along a curve of the type BCFG (Text-fig. 3).

Case III. Considering a more typical day and night cycle, if the water was initially saturated, then during eight hours' darkness the dissolved oxygen would fall to about 7.4 p.p.m. in accordance with curve AB (Text-fig. 3), deduced from Equation (7), but would recover during daylight to 9.2 p.p.m., to fall again at night to 6.9 p.p.m. Finally an equilibrium would be established in which the maximum concentration, C_D, during daylight and the minimum concentration, C_N, during the night would be given by the simultaneous equations,

$$\log_e \left(\frac{K(C_s - C_D) - K_1 - K_2}{K(C_s - C_N) - K_1 - K_2} \right) = Kt_1 \quad \ldots\ldots (12)$$

$$\log_e \left(\frac{K(C_s - C_N) - K_1 - K_2 + K_3}{K(C_s - C_D) - K_1 - K_2 + K_3} \right) = Kt_2 \quad \ldots\ldots (13),$$

where $t_1 = 8$ hours (darkness), $t_2 = 16$ hours, and the other symbols have the same significance and values as before. Thus $C_D = 8.9$ p.p.m. and $C_N = 6.6$ p.p.m. Therefore the addition of plants to the water under these conditions prevents the concentration of dissolved oxygen from becoming dangerously depleted.

It is not the case, however, that adding plants to an aquarium will necessarily improve conditions for fish. In certain circumstances the concentration of oxygen may fall during the night below the equilibrium (minimum) concentration C_E, attained in the absence of plants. This would be undesirable if, as a result, the concentration fell below the minimum that could be tolerated by the fish. By combining the equation

$$C_E = C_s - K_1/K \quad \ldots\ldots (14)$$

with Equations (11) and (12), the relation between C_E and C_N becomes

$$C_N = C_E + K_3/K\ [(1 - e^{Kt_2})/(1 - e^{24K}) - K_2/K_3] \quad \ldots\ldots (15)$$

where $C_N, C_E \geqslant 0$.

Thus, $C_N \geqslant C_E$, provided that $(1 - e^{Kt_2})/(1 - e^{24K}) \geqslant K_2/K_3$. The variation of the function $(1 - e^{Kt_2})/(1 - e^{24K})$, which for convenience will be denoted as F, with the over-all absorption coefficient, K, for three different values of the period of illumination, t_2, is shown graphically in Text-fig. 4(a). It will be seen that when the over-all absorption coefficient, K, exceeds the values 0.28, 0.19, and 0.12 (according as $t_2 = 16$, 12 or 8 hours), the function F becomes less than 0.1 and therefore, if, as we have assumed $K_2/K_3 \cong 0.1$, the expression $(F - K_2/K_3)$ becomes negative, so that the minimum concentration during darkness, C_N, falls below C_E.

It will also be evident that for any given value of K, the tendency for C_N to exceed C_E increases as the period of illumination increases, which is perhaps obvious without mathematical derivation. On the other hand the conclusion that the tendency for C_N to fall below C_E increases with increase in the absorption coefficient for solution of oxygen from the air, may at first sight appear more surprising. This arises, however, because for given values of K_1, K_2, and K_3, as the absorption coefficient is increased, the level of the dissolved oxygen concentrations approach nearer to the saturation value, and the amount of oxygen dissolved from the air during daylight may be small by comparison with that dissolved when, although the absorption coefficients are lower, the oxygen deficits are higher and *in proportion* are not reduced so much by the oxygen liberated in photosynthesis. Thus there is not so much opportunity to build up a "reserve" of dissolved oxygen when the absorption coefficient is high, so that when illumination ceases, the dissolved oxygen concentration may quickly fall below the equilibrium value, C_E, that would have been attained in the absence of plants. However, by the same token, as the concentration of dissolved oxygen falls, the oxygen deficit, and hence the rate of solution of oxygen, increases much more rapidly, in proportion, when the absorption coefficient is high than when it is low and the deficits are much greater, so there is less tendency for C_N to fall so far below C_E, when K is high. Substitution of the values for

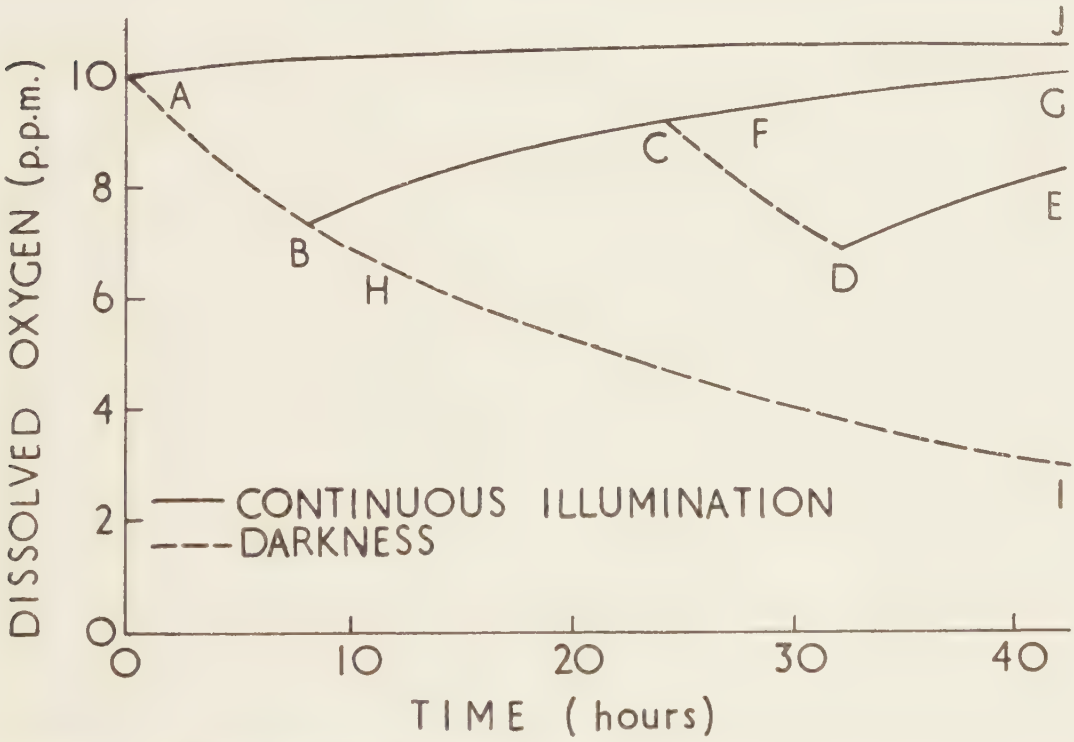
factor, F, from Text-fig. 4(a) in Equation (15) will show that, for given values of t_2, K_1, K_2, and K_3, as K is increased above the "critical values" at which $C_N = C_E$, then the difference $C_E - C_N$ at first increases (since the factor F decreases and $[F - K_2/K_3]$ increases) but then rapidly begins to decrease, since for values of $K > 0.5$, F becomes negligibly small and Equation 15 reduces to

$$C_E - C_N \cong 0.1\ K_3/K \quad \text{.....(15a)}.$$

It will also be seen from Equations (15) and (15a) that the difference, $C_E - C_N$, which is positive or negative depending on the value of K, increases directly in proportion to K_3, the rate of photosynthesis. For instance for $t_1 = t_2 = 12$ hours, $K_2/K_3 = 0.1$, $K = 0.1$, C_N exceeds C_E by 1 p.p.m., for $K_3 = 0.75$ p.p.m./h. and K_3 must be increased by 0.75 p.p.m./h. for each increase of 1 p.p.m. in the difference $C_N - C_E$. On the other hand, for $t_1 = t_2 = 12$ hours, $K_2/K_3 = 0.1$, $K = 0.5$, C_N falls below C_E by 1 p.p.m. when $K_3 \cong 10K \cong 5.0$ p.p.m./h., and for each increase of 1 p.p.m. in the difference, $C_E - C_N$, K_3 must be increased by 5.0 p.p.m./h. For the conditions cited in the example in Case III above we had $C_N - C_E = 3.8$ p.p.m. To make $C_N - C_E = 5$ p.p.m., say, it would be necessary to increase K_3 to 0.61 p.p.m./h.; that is, to increase the number of leaves of *Valisneria spiralis* from 70 to about 97.

To summarize, the major conclusion that may be drawn from the preceding discussion is that it is inadvisable to attempt to improve conditions in an aquarium having a moderate rate of solution from the air ($K \cong 0.3$ to 0.5) in combination with a relatively high rate of absorption by fish, by introducing a high rate of photosynthesis, since under these conditions the dissolved oxygen will fluctuate quite widely about an already low level and may well fall below the tolerance level at night.

Of course, it may be that fish can withstand and thrive in conditions in which the dissolved oxygen falls below the tolerance level for short



TEXT-FIG. 3. Effect of the respiration of fish and plants and the production of oxygen by photosynthesis on the concentration of dissolved oxygen in an aquarium.

Over-all absorption coefficient, $K = 0.05$/h.

Rate of consumption of dissolved oxygen:

by fish, $K_1 = 0.36$ p.p.m./h.,
by plants, $K_2 = 0.04$ p.p.m./h.

Rate of production of dissolved oxygen by photosynthesis: $K_3 = 0.44$ p.p.m./h.

periods but in which the daily average concentration is relatively high. Under such circumstances, the effect of introducing plants could be expressed in terms of the difference between C_E and the average concentration, C_A, given by $C_A = (C_N + C_D)/2$. (The true "time-average" concentration is rather complicated to work out but will not be greatly different from C_A.) The relation between the two can be shown to be

$$C_A = C_E + K_3/K\,[1/2\,(F_1) - K_2/K_3] \quad \text{.....(16)},$$

where $F_1 = (1 - e^{Kt_2})\,(1 + e^{Kt_1})/(1 - e^{24K})$. The variation of the numerical values of F_1 with variation in K, for three different values of t_2, is shown in Text-fig. 4(b). It will be seen that if $K_2/K_3 = 0.1$, $C_A > C_E$ under all conditions, since $F_1 > 0.1$, and $C_A - C_E$ may be increased by increasing t_2 or K_3. For $t_2 = t_1 = 12$ hours, $K_2/K_3 = 0.1$, then $C_A = C_E + 0.4\,K_3/K$ .....(17) so that to make $C_A - C_N = 1$ p.p.m., we must make $K_3 = 2.5$ K.

Limitations to the Kinetic Equations for Photosynthesis

In addition to the assumption already referred to on page 132, the kinetic equations for aquaria demand that (i) the water remains in the aquarium long enough for equilibrium to be established, (ii) that photosynthesis is independent of the degree of agitation of the water, (iii) that all the oxygen evolved is absorbed by the water, and (iv) that photosynthesis may be varied without restriction by changing the number or size of plants. These assumptions will be briefly considered:

(i). In a crowded aquarium, accumulation of noxious metabolic products may make frequent replacement of water necessary. In a sparsely populated aquarium or pond biochemical self-purification may considerably reduce the frequency with which replacement becomes necessary.

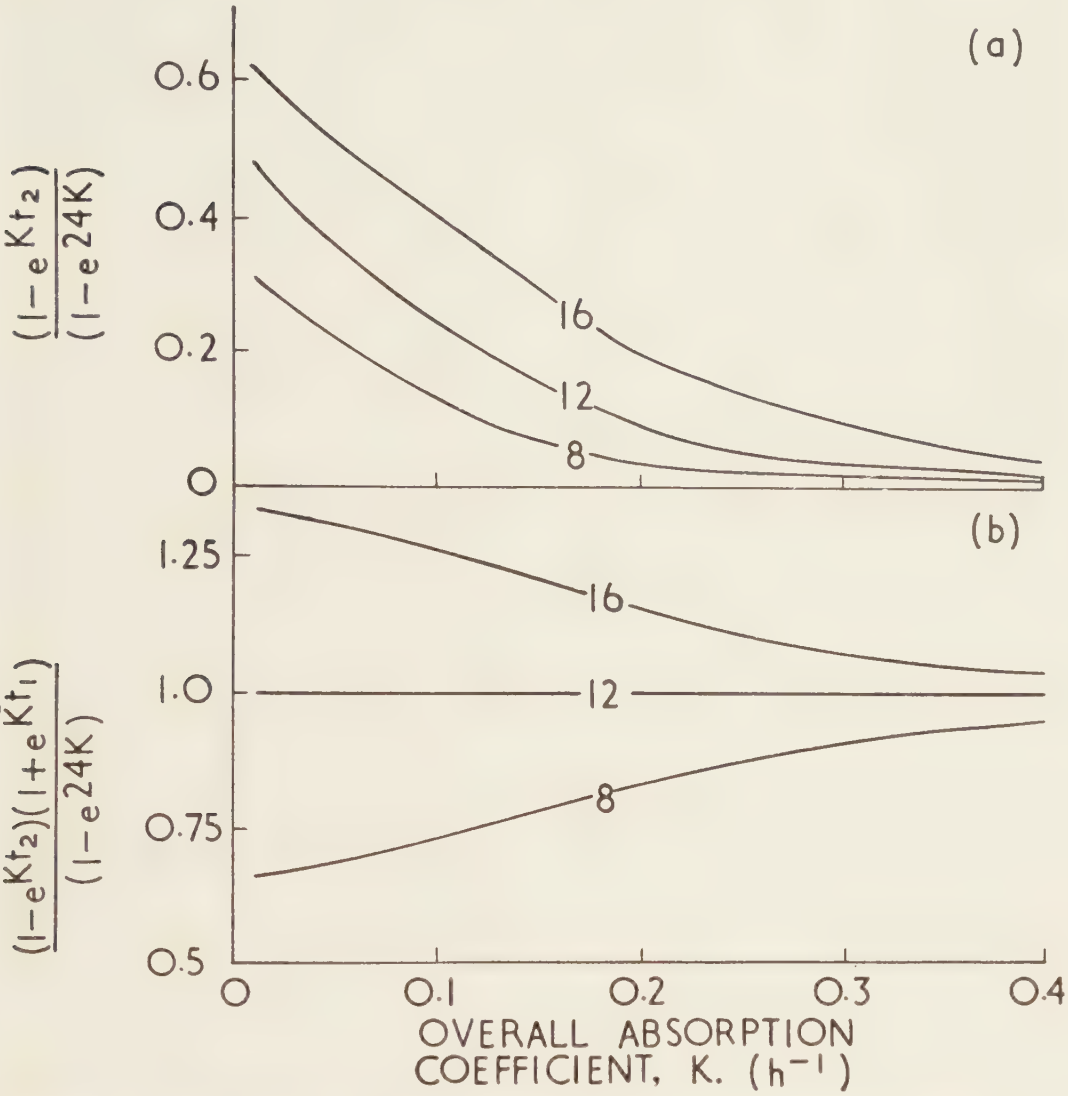
(ii). There appears to be no doubt that the rate of photosynthesis of aquatic plants depends upon the turbulence of the water, because of its effect on the rate of transport of carbon dioxide to the cells (Rabinowitch, 1951, Chapt. 27). Unfortunately, there appears to be little quantitative work on this subject, so for the present it must simply be noted as another variable to be considered.

(iii). When the rate of photosynthesis is high, oxygen may be liberated from the surface of aquatic plants in bubbles. The proportion of the liberated oxygen absorbed into the water will be a function of many factors, but it is doubtful if there is yet sufficient information to take this effect into account in aquaria.

(iv). In a given aquarium, the maximum rate of photosynthesis must inevitably depend on (a) the intensity of illumination and (b) the concentration and rate of supply of carbon dioxide.

(a). *Light intensity.*

It will be seen from Equation (11) on page 135 that 3.5 K cal. of energy are absorbed during the production of 1 gm. of oxygen. For a rate of production of oxygen of 1 p.p.m./h. (*i.e.*, $K_3 = 1.0$) in an aquarium, the equivalent rate of absorption of energy is about 84 gm. cal./litre, day. The daily amount of solar energy incident on a horizontal surface at sea level, of wave lengths which can promote photosynthesis and penetrate a smooth water surface, has been estimated by the U.S. Weather Bureau (Oswald & Gotaas, 1955). At latitude 52° the estimated monthly average amount of radiation in clear weather varies during the year from 21 gm. cal./cm.^{2}, day in December to 296 gm. cal./cm.^{2}, day in June; the corresponding average values for cloudy conditions are 4 and 176 gm. cal./cm.^{2}, day. If we consider a litre of water contained in a 10 cm. cube of glass the surface area will be 600 cm.^{2}, and assume that all this area receives radiant energy and neglect any absorption by the glass, the total amount of energy passing into the water will vary during the year from 21 × 600 to 196 × 600 gm. cal./day in bright weather, and from 4 × 600 to 176 × 600 gm. cal./day in cloudy weather. It has been calculated, however, that only some 2.0 per cent. of visible light incident on aquatic plants is utilized in photosynthesis (Rabinowitch, 1951, p. 1003), so that the net available energy for photosynthesis would vary during the year, taking the two extreme values, between 4 × 600 × 0.02 and 296 × 600 × 0.02 gm. cal./day, 10 cm. cube. If it is assumed that this energy is absorbed during 8 hours of daylight in December and 12 hours of daylight in June, the equivalent maximum rates of production of oxygen would be 3 × 4 × 600 × 0.02/84 = 1.71 p.p.m./h. and 2 × 296 × 600 × 0.02/84 = 85 p.p.m./h. However, the 10 cm. cube would be more similar in size to a gold-fish bowl rather than the average aquarium for which, as the size increased, the ratio of the surface area to volume would decrease, and also therefore the rate of increase of the concentration of dissolved oxygen. For instance, in an aquarium of the size of a 1 m. cube, the ratio of surface to volume would be only 1/10 that in the 10 cm. cube, and in consequence, other things being the same, the corresponding rates of production of oxygen would be 0.171 and 8.5



TEXT-FIG. 4. Values of functions in kinetic equations for photosynthetic production of oxygen. Period of daylight illumination, t_2, in hours shown against each curve.

(a) Variation of $\frac{1 - e^{Kt_2}}{1 - e^{24}}$ from the equation

$$C_N = C_E + \frac{K_3}{K}\left[\frac{1 - e^{Kt_2}}{1 - e^{24K}} - \frac{K_2}{K_3}\right]$$

with K and t_2.

(b) Variation of $\frac{(1 - e^{Kt_2})\ (1 + e^{Kt_1})}{(1 - e^{24K})}$ from the equation

$$C_A = C_E + \frac{K_3}{K}\left[\frac{1}{2}\left\{\frac{(1 - e^{Kt_2})\ (1 + e^{Kt_1})}{(1 - e^{24K})}\right\} - \frac{K_2}{K_3}\right]$$

with K and t_2.

p.p.m./h. In fact, however, the absorption of light by turbidity in the water and other "shading" effects would tend also to increase with increase in size (particularly with increase in depth), so that the actual practical values would be still further reduced. Despite this, it would appear that there is sufficient incident solar energy to support quite high rates of photo-

synthesis in summer, but that in winter, if one relies on daylight to provide energy, the maximum rate of photosynthesis is severely limited.

Carbon dioxide.

It is said that aquatic plants can assimilate carbon dioxide only in the form of neutral molecules, but there is also a possibility that in some cases bicarbonate ions may be utilized, although this contention has given rise to considerable controversy (Rabinowitch, 1951, Chapt. 27). According to Rabinowitch, the saturation level for carbon dioxide in photosynthesis occurs at concentrations in the range $1 - 10 \times 10^{-5}$ Molar, that is, 0.44 — 4.4 p.p.m.

Carbon dioxide is supplied to the aquarium by (i) absorption from the atmosphere, (ii) the dissociation and hydrolysis of bicarbonate and carbonate ions, and (iii) the respiration of fish and plants. The concentration and distribution of carbon dioxide between its various forms is governed by the constants of the following equilibria:

$$CO_2(g) \underset{k_s = 0.827}{\rightleftharpoons} CO_2(aq) \underset{k_{H_2O} = 2.2 \times 10^{-3}}{\rightleftharpoons} H_2CO_3 \underset{k_1 = 1.8 \times 10^{-4}}{\rightleftharpoons} H^+ + HCO_3^- \underset{k_2 = 5.61 \times 10^{-11}}{\rightleftharpoons} 2H^+ + CO_3^{--}.$$

N.B. Usually the apparent first dissociation constant, k_1', of carbonic acid is quoted as $k_1' = \frac{[H^+]\ [HCO_3^-]}{[CO_2] + [H_2CO_3]} = 4.54 \times 10^{-7}$.

If distilled water is allowed to come into equilibrium with normal air, it will be found to contain approximately 0.4 p.p.m. neutral carbon dioxide molecules (henceforth referred to as "free CO_2") and about 0.08 p.p.m. combined carbon dioxide present as bicarbonate ions. Owing to the small values of the constants k_{H_2O} and k_2, the quantities of carbonic acid and normal carbonate ion are negligible. Natural waters in equilibrium with normal air also contain about 0.4 p.p.m. free CO_2, but the amounts and proportion of combined carbon dioxide in the form of bicarbonate or carbonate ions depend on the pH value and alkalinity of the water. Since the concentration of free CO_2 is close to the lowest estimate of the saturation concentration for photosynthesis, it must be expected that removal of free CO_2 will tend to bring about a decrease in the rate of photosynthesis unless other factors are limiting. However, removal of free CO_2 will displace the CO_2-equilibrium and cause ionized carbon dioxide to recombine to form carbonic acid which dissociates to free CO_2, and additional carbon dioxide then dissolves from the air. This "resistance" to changes in carbon dioxide concentration, and hence to changes in the rate of photosynthesis, will increase with increase in the total combined carbon dioxide concentration, but will be governed by the rate at which the reactions influencing the equilibria take place; that is, by the rate at which carbon dioxide is made available by the processes (i), (ii) and (iii) above.

(i). If the exit coefficient for carbon dioxide is approximately the same as that for oxygen (a reasonable assumption for natural waters or tap waters but not necessarily for very alkaline solutions), then the maximum rate of supply of carbon dioxide from the air will be K times the equilibrium concentration of free CO_2, *i.e.*, 0.4K p.p.m./h. Therefore, unless the rate of aeration is relatively large, the supply of carbon dioxide from the air will not support a very high rate of photosynthesis.

(ii). When free CO_2 is removed from the system, it can be replaced by the dissociation of carbonic acid and, it is said, bicarbonate ion (Rabinowitch, 1951, Chapt. 27) in accordance with the reactions

$$H_2CO_3 \underset{k_A = 10/\text{sec.}}{\rightleftharpoons} H_2O + CO_2$$

$$HCO_3^- \underset{k_B = 0.47 \times 10^{-4}/\text{sec.}}{\rightleftharpoons} OH^- + CO_2.$$

For a water in equilibrium with the air, the concentration of carbonic acid is $0.4k_{H_2O} = 0.4 \times 2.2 \times 10^{-3} = 8.8 \times 10^{-4}$ p.p.m. Assuming that the reactions $H^+ + HCO_3^- \rightarrow H_2CO_3$ and $H^+ + CO_3^{--} \rightarrow HCO_3^-$ are virtually instantaneous, the maximum rate of supply of carbon dioxide from this source is therefore $8.8 \times 10^{-4}\ k_A$ p.p.m./sec. = 31.6 p.p.m./h.

The maximum rate of supply from the dehydration of bicarbonate ions will be $0.47 \times 10^{-4} \times 3.6 \times 10^3$ p.p.m./h., p.p.m. $HCO_3^- =$ 0.169 p.p.m./h., p.p.m. HCO_3^-. Thus for a concentration of bicarbonate of 100 p.p.m. this corresponds to a rate of supply of 16.9 p.p.m./h.

These rates will tend to fall as carbon dioxide is removed from the system, since apart from the fall in the total concentration of carbon dioxide, the pH value will rise and in consequence the proportions of carbonic acid and bicarbonate will decrease. Ultimately if this trend continues and the water contains calcium ions, calcium carbonate will be precipitated so that some of the combined carbon dioxide hitherto available for photosynthesis will be effectively lost from the system. In a natural water containing an average concentration of combined carbon dioxide of the order of 100 p.p.m. or more, these changes will come about

slowly, and reasonably high rates of photosynthesis should be feasible for long periods. In distilled water, however, changes in the concentration of carbonic acid and bicarbonate ion will be directly proportional to the loss of carbon dioxide from the system, and since the total concentration initially present in water in equilibrium with the air is only about 0.5 p.p.m., even a comparatively low rate of photosynthesis may soon be restricted for lack of carbon dioxide.

Taking all these factors into account, it would seem reasonable to expect the supply of carbon dioxide from ionic dissociation to support continuously a rate of photosynthesis of at least $K_3 \cong X/24t$ p.p.m./h. where X p.p.m. is the total concentration of carbon dioxide in all forms and t is the period between replacement of the water, provided that other factors are not limiting and that K_3 does not exceed a value $K_3 \cong 31.6 + 0.169\ [HCO_3^-]$ p.p.m./h.

(iii). Fish and the plants themselves are the main respiring organisms to be considered in the aquarium. Since the respiratory quotient for fish is about 0.7 — 1.0 and one volume of oxygen is liberated per volume of carbon dioxide absorbed in photosynthesis, the maximum rate of photosynthesis from carbon dioxide produced from fish absorbing oxygen at K_1 p.p.m./h. will be $K_3 \cong 0.7 - 1.0K$. Plants will provide carbon dioxide at a rate K_2 equal to the rate of respiration.

If now we assume that the limiting rate of photosynthesis, K_3^L, in aquaria due to restriction in the supply of carbon dioxide is given by the sum of the individual maximum rates of supply due to (i), (ii) and (iii) above, we have

$$K_3^L = K_1 + K_2 + 0.4K + \frac{X}{24t}.$$

Thus if K, K_1, and K_2 take the values 0.05, 0.36, 0.04 as in previous examples, X = 240 p.p.m. (a reasonable value for tap water or natural fresh water) and t = 5 days we have

$$K_3^L = 0.36 + 0.04 + 0.4(0.05) + \frac{240}{24 \times 5} = 2.42 \text{ p.p.m./h.}$$

It will be noticed that although this rate is somewhat lower than the limiting rate for summer conditions, it is somewhat greater than the calculated limiting rate of photosynthesis caused by the low level of daylight illumination in winter. Thus the indication from these approximate calculations is that the maximum rate of supply of oxygen by photosynthesis may under some circumstances in the summer be limited by the supply of carbon dioxide rather than the intensity of illumination.

More Complex Systems

The only systems considered have been those in which the absorption or production of oxygen, apart from that due to atmospheric aeration, was a linear function of time and was independent of other variables. There is, however, no *a priori* reason for this other than shortage of detailed information about photosynthesis and respiration, and it should be possible to formulate equations representing the variation of dissolved oxygen with time, if, as information accumulates, these factors prove to be more complicated functions. As a simple example of a more complex system (in the mathematical sense, that is), we may consider the case in which the water in the aquarium has a biochemical oxygen demand (B.O.D.) exerted at a rate such that

$$L_t = L_0 e^{-kt} \qquad (18),$$

where L_0 and L_t are the ultimate B.O.D.'s at times 0 and t hours and k is the velocity constant. This situation may well occur in work on the toxicity of effluents, or in aquaria or ponds in which dying plants are present. If absorption by fish is constant, K_1 as before, and $K_2 = K_3 = 0$, then

$$\frac{dC}{dt} = K(C_s - C) - K_1 - kL_0 e^{-kt} \qquad (19)$$

$$\text{and } C = \frac{k}{K-k} L_0 (e^{-Kt} - e^{-kt}) + C_0 e^{-Kt} + \frac{(KC_s - K_1)(1 - e^{-Kt})}{K} \qquad (20).$$

In this case, the oxygen concentration would pass through a minimum, C_M, given by

$$C_M = C_s - \frac{(kL_0 e^{-kt_M} + K_1)}{K} \qquad (21)$$

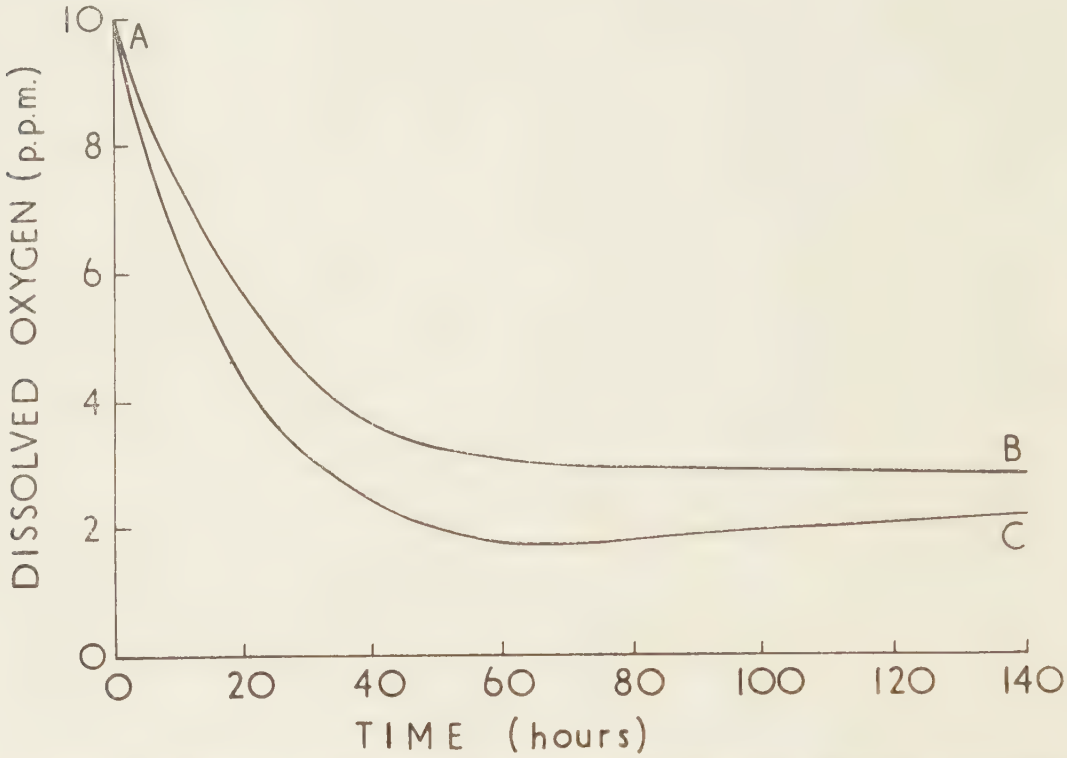
at time

$$t_M = \frac{1}{K-k} \log_e \left[\frac{K}{k} - \frac{K(C_s - C_0) - K_1(K-k)}{L_0 k^2} \right] \qquad (22)$$

before finally reaching an equilibrium given by

$$K(C_s - C) = K_1.$$

Suppose, for instance, that in addition to the consumption of oxygen by fish at a rate $K_1 =$ 0.36 p.p.m./h., when the rate of reaeration is 0.05/h. (as in curve AB, Text-fig. 5), the water contains an initial ultimate biochemical oxygen demand, L_0, of 10 p.p.m. and that the velocity constant of the B.O.D., k, takes a value of 0.01/h. (Phelps, 1947). If these values are then substituted in Equations (20), (21) and (22), it will be found that the dissolved oxygen will fall to a minimum concentration of 1.77 p.p.m. in 67 hours before gradually recovering to the



TEXT-FIG. 5. Effect of the respiration of fish and of a biochemical oxygen demand on the variation of concentration of dissolved oxygen in aquaria.

Over-all absorption coefficient, K = 0.05/h.

Rate of consumption of dissolved oxygen by fish, K_1 = 0.36 p.p.m./h.

Initial ultimate biochemical oxygen demand, L_0 = 10 p.p.m.

Velocity constant of B.O.D., k, = 0.01/h.

Curve AB: L_0 = 0.

Curve AC: L_0 = 10 p.p.m.

equilibrium concentration of 2.8 p.p.m. in accordance with curve AC, Text-fig. 5. The chosen value for L_0 is, of course, quite low and could easily be exceeded—for instance in a pond in which there had been a profuse growth of plants during the summer, most of which died and decayed at the onset of colder weather. In such a case, the water might be completely depleted of oxygen and therefore quite unsuitable for fish.

DISCUSSION

Methods for determining the rate of solution of atmospheric oxygen in water and the use of these data in the formulation of simple equations expressing the variation with time of the concentration of dissolved oxygen in aquaria have been described. These equations are based on a number of simplifying assumptions and approximations either because more detailed information is not available or because a more rigorous treatment has not been justified in view of the considerable variability of living organisms. It may well be a chimera to suppose that even with a great deal more information on some of the variable factors, it will be possible to make better than semi-quantitative predictions about variations in the dissolved oxygen content of aquaria, except perhaps in simple systems under rigidly controlled conditions. It is, however, difficult in the present state of knowledge to foresee to what extent more accurate information will be required. Meanwhile it is hoped that the present simple treatment will serve as an introduction to the subject to those who are unfamiliar with the general principles of the "dynamics of aeration," and will also prove a useful starting point

for anyone contemplating a detailed study of the part played by carbon dioxide in aquaria.

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Reproduction in the King Cobra, *Ophiophagus hannah* Cantor

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(Plates I-V)

INTRODUCTION

THE King Cobra (*Ophiophagus hannah* Cantor), the longest venomous snake in the world and one of the very few occasionally aggressive species, is one of a small number of snakes that guards the eggs during incubation, and is the only snake known to deposit its eggs in a nest made of vegetable matter. A good deal has been written about each of these attributes, but little is known of the details of the reproductive habits of the species.

That a snake constructs a sizeable nest of vegetable material is difficult to imagine. Colonel Frank Wall summarized the knowledge about this snake up to 1924 and concluded, "It seems most probable she selects a chance accumulation of debris which she can appropriate for her use." Wall also pointed out that little is known of the courtship, period of gestation or period of incubation in this species. He did report the killing of two pairs in the act of mating, one in March and the other in late April or early May, but gave no additional details. Little additional information on these topics has been published since the date of Wall's paper.

Wasey (1892) appears to be the first to report the deposition of eggs in a nest and the guarding of eggs. He killed a snake 9 feet 8 inches long on "a heap of dried leaves," at the bottom of which he found 33 eggs. Fenton (1917) reported finding an individual, also of unspecified sex, 9 feet 3 inches long, on a mound of leaves 2 feet high and 8 or 9 feet in circumference. He failed to note any eggs. H. C. Smith (1936) described a nest in detail and included a photograph of the nest, eggs and the dead snake, which was not sexed but measured 7 feet 5 inches. The nest contained 27 eggs and was a compact mass of dead leaves measuring 1 foot 7 inches in diameter and 9 inches deep. The eggs were covered with a layer of leaves that formed the bottom of the upper depression of the nest on which the snake was resting when discovered. Mustill (1936) described a nest observed by him in 1926. This contained 40 eggs and was guarded by a snake that measured "about 12 feet in length." The nest "was built in the base of a small shrub about 6 inches from the ground and at first sight it resembled the nest of an English magpie. It was composed of sticks and other debris and contained a hole in the top through which the snake could pass." Mustill estimated the nest to be 2 feet from top to bottom and about 2 feet 6 inches in diameter. He noted an upper and lower chamber, with the eggs in the latter and the snake resting in the former.

King Cobras in the collection of the New York Zoological Park have provided data on the reproductive habits of this interesting species. Three specimens were obtained from a dealer in Bangkok, Thailand, and reached the Park on October 10, 1953. At that time the larger male measured 14 feet 6 inches, the smaller male 11 feet 2 inches and the female 13 feet 4 inches. The snakes were kept in temporary quarters until April of 1954 when they were moved to their permanent home in the newly renovated Reptile House. Here the three snakes were placed in a cage 7½ feet long, 6½ feet wide and 6½ feet high. The cage is provided with a large water pool approximately three feet long and two feet wide. In one corner of the cage there is a raised planted area, containing small bamboo stalks with leaves. Several vertical sticks of bamboo are set in the floor of the cage for decorative purposes and are on the opposite side. A shift cage 6 feet long and 2 feet wide adjoins the main cage but is not visible to the public. The door to this cage is usually left open, permitting the snakes free access except when

it is desired to isolate one or more for feeding or some other reason. The shift cage provides the snakes with an area of seclusion from the public, although rarely do all three retire to the shift cage at the same time.

The floor is heated by hot water pipes located in the floor across the front of the cage. This provides a thermal gradient from the front to the back of the cage. The average temperature is between 27° C. and 30° C., with the front area being two or three degrees warmer than the rear. The floor is covered with white crystalline sand, from a half to an inch in depth. In the right rear corner there is a small pile of bamboo leaves and stalks. This is a favorite resting place of the three snakes and is the spot in which the nest has been built each year. The cage is lighted with incandescent lights, but also is provided with ultraviolet light that is turned on for daily intervals of 15 to 30 minutes.

The King Cobras are fed an average of once a week on dead snakes that have been frozen and thawed. Many species of snakes have been used as food in this manner, including boids, colubrids, viperids and crotalids. Once the cobras were accustomed to this type of food, they refused live snakes and would eat them only after they had been killed.

In 1955 and 1956 the smaller male and the female mated and the female laid eggs. Observations were made on these activities each year and both still photographs and motion pictures were obtained. I am grateful to Sam Dunton, Staff Photographer at the New York Zoological Park, for his cooperation and patience in getting an excellent photographic record. Head Keeper Stephen Spencook and Keepers Peter Brazaitis, Raymond Cummins and Robert Raabe all assisted greatly in recording the data reported herein and have my sincere thanks.

Courtship and Mating

Early in March of 1955 the larger male and the female were observed in intermittent courtship activity, but no record was made of the duration or exact nature of the activities and no mating was observed. On March 10, 1955, I observed the smaller male and the female in courtship. When first noted at 12:30 p.m. the female was crawling slowly around the cage. Her head and neck were raised obliquely about ten inches above the floor and her hood was spread (Fig. 1). The male was on top of the female with his head about three feet behind hers. He was moving forward along her back with his tongue flicking out frequently. When his head reached the hood of the female, he gently nudged her hood and head several times with his nose (Fig. 2). The male constantly flicked his tongue on either side of the female's head (Fig. 3). During the entire process both snakes crawled slowly around the cage,

The rear half of the male's body looped back and forth on either side of the female's body and slowly moved backward and forward as the two crawled along. The male occasionally slid off the female, at which time his head explored along her sides, nudging her. She paused several times and as soon as she started crawling again the male regained his position on top of her, usually about mid-body. His head quickly moved forward along her back, nudging her body with his snout as he moved along her back and continually flicking his tongue on her skin.

The female appeared to stimulate the male by merely crawling slowly away from him. When the female stopped crawling or if she attempted to coil, the male nudged her body sharply with his snout (Fig. 4). Either individual seemed able to initiate courtship. At the beginning, the male appeared to be stimulated visually and throughout courtship by chemical stimuli perceived through the tongue-Jacobson's organ system and possibly some tactile stimulation. In contrast the female appeared to respond primarily to tactile stimulation alone. Sex recognition probably involves visual and chemical cues, as well as behavior. Whenever the smaller male was actively prowling about the cage and touched the larger male, the latter reared, spread his hood and made threatening jabs that seemed to divert him. When the smaller male came upon the female, she would lie still until he pushed her vigorously with his head, or sometimes immediately start to crawl away, whereupon he would attempt to court her.

After the pair had courted for about thirteen minutes and shortly after a series of gentle nudges by the male, he lifted the rear of her body with his tail, brought his vent under hers (Fig. 5) and both hemipenes were everted about an inch but quickly withdrawn. Courtship was resumed and after another three minutes the male again raised the base of the female's tail. At this time his vent was approximately opposite and under hers but on the right side. His left hemipenis only was everted and copulation was effected. Immediately all movement stopped and the pair remained motionless for the next 15 minutes. Slowly the male moved off of the female so that the two were headed in opposite directions. The male tried to pull away, but the female began to crawl slowly, taking the male with her (Fig. 6). The two remained in contact for 57 minutes, after which time they separated, each going to opposite sides of the cage.

The temperature in the cage at the time of this mating was 27.5° C. (82° F.). The day was

clear and mild with an outdoor temperature of 21° C. (69° F.). A crowd of fifteen to twenty persons gathered in front of the cage from time to time but the snakes appeared completely undisturbed.

On two other occasions in 1955 this same pair was observed in a mating union when the keepers entered the Reptile House in the morning; once at 7:21 a.m. on March 14 and again at 7:23 a.m. on March 18. On neither of these days was the complete time of mating recorded, since the snakes were already in contact when noted. On the 14th the snakes separated at 8:07 a.m. and on the 18th at 7:31 a.m.

In 1956 the smaller King Cobra engaged in courtship with the female for several minutes on January 6, but no mating occurred. Courtship again occurred on January 12. On January 16 vigorous courtship took place for 22 minutes and culminated in mating.

On January 17 the same pair commenced courting at 9:40 a.m., during which time the male made three efforts to insert the hemipenes into the female. At 10:00 a.m. a successful union was made. As in the previous matings, all movement stopped as soon as one of the hemipenes was inserted. On this occasion copulation lasted 58 minutes, during the latter half of which time the female crawled around slowly, pulling the male with her. Fifty minutes after the union was effected and while the two snakes were still in copulation, the male was in the vicinity of the water pool and took a long drink. Throughout this courtship and mating the cage was brightly illuminated by photoflood lights, which appeared to have no effect on the snakes.

On January 26, the smaller male and female were observed in copulation at 8:31 a.m. They parted at 9:37 a.m. During the night of February 17 this pair shed their skins. About 3:00 p.m. on February 18, the two males participated in a brief and incomplete "combat dance." Each reared the anterior portion of its body and entwined it with that of the other while making short jabs with its head at its opponent's head. They separated after a minute or two and the larger male attempted to court the female, but was driven away by the smaller male. The latter courted the female and mating took place at 3:24 p.m. This union was broken at 4:23 p.m. After being driven away by the smaller male, the larger male remained quietly in a corner of the cage, apparently indifferent to the mating pair.

On March 8 and 14 the smaller male and female were observed mating, between 8:20 a.m. and 9:00 a.m. on the former occasion and between 8:05 and 8:55 a.m. on the latter. The start of neither of these matings was noted. Courtship and mating in all of the observed instances followed the pattern reported in detail for March 10, 1955.

Nest Building

The building of the nest was observed and photographed both years. In anticipation of this activity, freshly cut bamboo stalks were laid around the floor of the cage, and each year after the female began to build her nest, additional bamboo and some large dead magnolia leaves were introduced into the cage away from the side of the nest.

On April 21, 1955, at 7:40 a.m. the female was observed pushing the bamboo litter of the floor into a compact pile near the center of the cage. This was done by crawling part way around a pile of litter and then drawing the head and body back in an open loop. Between 8:00 a.m. and 9:00 a.m. she moved this pile into the rear corner of the cage behind several vertical sticks of bamboo. She soon had virtually all of the bamboo stalks back in the corner and began pushing sand on the pile. This was done by tilting the head about 45° to one side and pushing it through the sand for a short distance, then dragging the loosened sand back on the inside of an open loop. Moving the bamboo litter and the sand were both accomplished by movements that resulted in the anterior one-third to one-half of the body being employed as a large hook used on its side to drag in the loose material.

At 9:20 a.m. additional stalks of bamboo were spread around the floor of the cage and the two males were removed. (They were not returned to the cage until after the eggs had been removed on May 4, 1955). Neither had made any movement until just prior to this time, when the smaller male tried to crawl onto the growing heap of bamboo stalks. The female drove him away with two quick and forceful jabs of her head. This appears to be the customary method of avoiding intrustion or rejecting advances. I have seen these snakes use this movement many times when excited. The mouth is kept closed and the snake strikes out sharply with the head. It is a more forceful movement than the gentle jabs of courtship.

After driving away the male, the female rested on top of her pile of bamboo, lying in an elongated coil that covered the entire pile. She remained in this position with little movement until 3:30 p.m. when she began moving more bamboo toward the nest pile. At this time several clumps of dried magnolia leaves were put on the floor, but she ignored them. She coiled up on top of the pile again at 4:10 p.m. and remained quiescent the rest of the day.

Keeper Raabe came in early on the morning

of April 22. Before he turned on the lights at 7:16 a.m. the female was resting quietly on top of the pile of bamboo. As soon as the lights were turned on, she moved off the pile and started dragging in a clump of magnolia leaves. These were drawn to the top of the pile on the inside of a loop of her body held close against the floor of the cage. At 7:24 a.m. she crawled into the pile and began pushing out a chamber from the inside. She crawled round and round in a tight coil inside of the nest, sometimes pausing to push out a loop of her body to pack down the bamboo and leaves. Once she pushed the loop out with her head. After several minutes of this she emerged from the nest part way and, using her head to loosen the sand, drew some sand in on the pile of leaves.

Without resting, she crawled farther out into the cage, entwined her body through several bamboo stalks that were together and pulled them back in a loop of her body (Fig. 7). Then she went out and drew her body around a pile of magnolia leaves, which she dragged back with the forward part of her body (Fig. 8). She retired again to the center of the nest and, coiling tightly, revolved around in the middle of the structure, pausing occasionally to thrust the leaves and stalks back with a loop of her body. These movements became quite jerky and she appeared to be exerting considerable force to form the inner chamber of the nest. It became increasingly difficult to observe her movements since the nest had become quite large and most of her body was not visible when she retired into it. In entering and leaving the nest pile the female followed no regular path. One time she would enter from the side and go under or into the accumulated material. The next time she might go on top of it. She never entered from the front, but always from one side or the other. When the nest was nearly completed she appeared to go to the top of the pile rather than in the sides.

At 7:44 a.m. she again emerged from the nest, crawled out and around a pile of leaves she had previously moved into the corner of the cage. With her body looped tightly around this bunch of leaves she literally carried them to the pile, holding the coil about two inches off the ground. These were pulled inside the nest and she again revolved several times in a tight coil. Some leaves dropped out of her coil as she tried to pull them inside. She soon emerged and continued dragging in stalks and leaves. At 8:50 a.m. additional bamboo and magnolia leaves were placed around the floor of the cage. At this time the snake was spending longer and longer periods of time shaping the interior chamber and was almost entirely hidden from view. Occasionally she would come out and drag in small amounts of additional material.

At 10:00 a.m. the female emerged from the nest and crawled to the water pool where she took a long drink. She rested awhile beside the pool and then retired into the nest. Little movement of any sort was noted until shortly after 1:00 p.m. when she again began revolving inside the nest, making jerky pushes outward with a loop of her body. These movements lasted less than 15 minutes, after which time she remained quietly in the nest. No activity of any sort was observed on the 23rd of April, and the eggs were laid on the morning of the 24th. After the eggs were all laid in the central chamber, the female moved leaves over them and almost completely covered them with a layer of litter (Fig. 9). She then coiled on top of the leaf-covered egg heap. This is probably the basis for the statements of H. C. Smith and Mustill that the nest is divided into an upper and a lower chamber, with the eggs deposited in the latter and the snake resting in the former.

In 1956 the female started building her nest on the morning of April 20, almost exactly one year from the date she started her nest in 1955. The method of dragging in leaves and stalks was the same as that employed the previous year. The female worked on and off all day the first day and most of the second. During both days the cage was lighted by photoflood lights to permit the taking of motion pictures. The following morning the female tore the nest apart in some unobserved fashion, scattering many of the leaves and stalks all around the cage. She commenced to rebuild it shortly after 8:40 a.m. and completed the job on the afternoon of April 23. In the rebuilt nest the inner chamber was located about one foot away from where it had been situated in the two previous nests, and was shallower. The eggs were laid on the morning of April 24, the same date as in 1955. This time, possibly because of the shallower chamber, the female did not cover the eggs completely and coiled her body partly around the uppermost eggs.

Eggs

It is impossible to determine the period of development of the eggs since there is no way of knowing accurately when they were fertilized. In 1955 three matings were observed, all in March within a period of nine days. Whether or not there were other matings is unknown. In this year the eggs were laid approximately six weeks after the first recorded mating and about five weeks after the last. In 1956 the pair was observed mating on six occasions over a period of approximately sixty days. The last two mat-

ings, on March 8 and 14, fall within the period of the three observed the previous year and would give a developmental period of five to six weeks.

In their studies on reproduction in the Garter Snake (*Thamnophis sirtalis*), Frank N. and Freida Cobb Blanchard (1941) found that very early matings were not followed by correspondingly early births. Late April seemed to be the invariable start of the period of development. This, they inferred, was related to the arrival of more or less continuously warm weather. Such would not appear to be the case with snakes kept indoors at more or less constant temperatures all year. It is unwise to speculate on the basis of data from only two years, but it is interesting to contemplate whether the deposition of eggs on the same date each year is coincidental or the result of some regulatory factor.

In 1955 part or all of the egg clutch had been laid by 7:45 a.m. when Head Keeper Spencook checked the nest. Eggs were visible in the center of the nest at that time. The female continued to move around in the center of the nest, but we were unable to determine definitely whether she was continuing to lay eggs or simply covering them. Around 10:00 a.m. she became quiet, resting near the top of the central chamber with only part of her body visible. No eggs could be seen at this time. At 1:00 p.m. the leaves covering the chamber of the nest were gently lifted away so that photographs could be taken. As soon as we tried to uncover the eggs the female quickly covered them again with leaves or her body. She usually brought her head around quickly to wherever the leaves were removed and would push other leaves over the exposed eggs.

In order to photograph the eggs in the nest and to count and measure them, the female was removed from the nest and restrained behind a large plastic shield. After counting, 14 of the eggs were replaced and the shield was withdrawn. She immediately returned to the nest, covered the eggs and resumed her resting position in the upper part of the nest.

In 1956 all of the eggs had been laid by 8:00 a.m. when the nest was checked. Again most of the eggs were taken out of the nest, but five were returned. The female again covered these eggs and coiled on top of them.

The number of eggs previously reported in the literature varies from 21 to 40. In 1955, the female laid a total of 41 eggs, of which 11 were abortive. The abortive eggs were one-half to two-thirds the size of the normal ones and were covered with a more pliable shell. In 1956 a single small abortive egg was found on the floor of the cage each morning on April 17, 19 and 21. Sometime during the early morning of April 24 an additional 48 eggs were laid in the nest, making a total of 51. An exact count was not made of the abortive eggs in this clutch, but approximately forty appeared to be of that nature and soon spoiled. The remaining eggs became moldy and were destroyed.

Ten of the normal-appearing eggs of the 1955 clutch were weighed and measured the afternoon on which they were laid. The data obtained were as follows:

April 24, 1955

Egg No.	*Weight (in grams)*	*Length (in mm.)*	*Width (in mm.)*
1	40.0	60.0	34.0
2	40.0	57.7	34.3
3	40.5	58.1	35.0
4	40.0	57.6	34.6
5	42.5	58.5	32.8
6	41.0	58.8	35.0
7	40.5	59.2	34.8
8	42.8	64.3	34.6
9	40.9	63.2	32.3
10	40.3	58.1	36.0

The eggs removed from the nest were divided into three lots: one for incubation in leaf litter, one for incubation in damp sawdust and one for incubation on moist paper towels. The ten eggs that were weighed and measured were placed in damp sawdust. These were weighed and measured on three subsequent occasions, as follows:

May 23, 1955

Egg No.	*Weight (in grams)*	*Length (in mm.)*	*Width (in mm.)*
1	51.0	61.5	38.1
2	50.5	61.2	38.9
3	46.5	64.7	35.1
4	50.0	59.3	39.5
5	47.5	62.8	36.2
6	51.0	61.1	38.6
7	51.5	62.6	36.3
8	54.5	61.9	40.1
9	57.0	60.4	41.6
10	57.2	62.1	41.5

June 14, 1955

Egg No.	*Weight (in grams)*	*Length (in mm.)*	*Width (in mm.)*
1	56.5	61.2	41.2
2	55.3	60.8	40.0
3	50.5	64.9	36.1
4	53.0	58.7	41.0
5	50.7	61.8	38.8
6	56.2	61.2	41.0
7	54.5	63.3	38.1
8	59.5	61.5	41.7
9	73.3	63.7	46.8
10	74.0	65.4	46.5

JULY 5, 1955

Egg No.	Weight (in grams)	Length (in mm.)	Width (in mm.)
1	58.0	61.5	41.3
2	62.0	61.5	43.8
3	52.0	65.0	36.7
4	57.0	59.4	40.8
5	58.0	64.6	41.1
6	82.0	65.8	48.0
7	75.0	66.8	44.1
8	71.0	63.7	44.5
9	hatched	—	—
10	96.0	70.8	49.5

At 4:00 p.m. on July 4, egg No. 9 had a slit in the shell and the hatchling had its head and about 1 inch of the body protruding through the slit. The snakeling emerged sometime during the night. It measured approximately 460 mm. in total length and weighed 23 grams. During the following nine days thirteen other youngsters emerged, but four of these were crippled by deformities of the spinal column. Thus a total of nine healthy-looking youngsters were obtained from the clutch.

The period of incubation before the first egg hatched was ten weeks and one day, and the total period until the hatching of the last egg was eleven weeks and three days. During incubation the ten measured eggs increased an average of 66.1% in weight, 8.1% in length and 26.2% in width.

No data are available on the weights, measurements or incubation period of the eggs in the 1956 clutch.

GUARDING THE NEST

Early reports on the discovery of nests of King Cobras invariably include a guarding parent. Although the sex was not determined in any of the reports I have seen, Wall (1924) says, "All those who have met the hamadryad during the period of incubation have remarked upon the fact that the female has been coiled up on a nest of leaves, or vegetable rubbish." It appears to have been a common assumption that the guardian snake was the female, but whether this is invariably so or not I do not know.

In 1955 after the female had been moved off of her nest so that we could examine the eggs, she returned to it the afternoon of April 24 and remained coiled on the eggs until 4:40 p.m. on April 28 when she left and went to the water pool to take a long drink. The remaining eggs were removed from the nest on May 4 because they were becoming covered with mold. The female remained on the nest for a day or two longer, but the two males were returned to the cage and the nest was soon matted down into a common resting site for all three snakes. The female left the nest on May 4 to take her first meal since building it.

On April 25, 26 and 27, while the female remained on the nest, temperature readings were taken of the cage floor immediately beneath the nest, the interior of the egg cluster, between the coils of the snake, and the air one foot above the nest. These readings were taken with a Schultheis thermometer graduated in .2° C. There was not more than .4° C. difference in any of the readings, which were 27.4° to 27.8° C., and no constant pattern was noted in the differences. From these observations it is concluded that the presence of the female in the nest causes no rise in temperature that would aid the incubation process. Rather, her role in remaining with the eggs appears to be solely one of protection.

Many of the reports of unprovoked attacks by this snake attribute particular aggressiveness to the female when guarding her nest. Thus Wall (*op. cit.*) says, "The female when disturbed in the process of brooding her eggs, seems to be specially sensitive, and usually attacks the intruder at sight." This may be an exaggeration. There is no doubt that these snakes are sometimes aggressive, but whether this is the exception or the rule is open to question. G. H. Evans (1921) reports an encounter with a large King Cobra that was intent on escaping and made no effort to attack despite considerable provocation. He concluded with the remark, "I am more than ever convinced that hamadryads as a rule are as glad to escape as most other snakes." H. C. Smith (1936), referring specifically to a guardian snake on a nest close to a forest path, wrote, "It is interesting to note that fourteen people accompanied by seven dogs twice passed at different times within two yards of the nest and yet the hamadryad failed to show itself and the nest remained undiscovered until I prodded the heap of leaves with a small cane."

The three snakes whose activities are reported here were quite aggressive when they came to the Zoological Park, but, like most snakes under proper conditions of captivity, they became accustomed to the presence of visitors and keepers. By 1955, when the first matings occurred, none of the three seemed to pay attention to the keepers cleaning their cage except to investigate movements or cleaning implements. The snakes would not spread their hoods unless aroused vigorously. So far as we could tell, there was no change in disposition on the part of any of the snakes during the period of courtship and mating nor on the part of the female while guarding her nest, although the males were somewhat more alert to movements and were more active during this time. When the female was disturbed on her nest she appeared more concerned with

covering her eggs than with trying to drive off the intruder. Even when she was removed from the nest forceably to enable us to take out the eggs, she made no effort to strike or bite.

Young

The nine healthy young snakes, six males and three females, were marked very differently from the adults (Figs. 11 & 12), as had been noted by Wall (*op. cit.*).The ground color was black. This was interrupted by a series of narrow white to yellowish-green cross-bands approximately one scale wide and separated by spaces three to four scales wide. The scales bordering the light bands were mostly solid black, whereas those inside the dark interspaces were light in the center. The snout was white to yellow, with a narrow black band across the sutures of the internasals and prefrontals, extending ventrad onto the labials. There was a broader supraocular black band followed posteriorly by a narrow yellow area. The first of the black interspaces was on the rear of the head and neck.

The young varied from approximately 460 to 640 mm. in total length and in weight from 19 to 26 grams. They quickly assumed a defensive attitude when disturbed and struck vigorously if approached too closely (Fig. 12). They refused all food offered them and lived only four or five months. The food offered them included earthworms, mealworms (*Tenebrio*), Red-backed Salamanders (*Plethodon cinereus*), Red Efts (*Diemictylus v. viridescens*), American Toads (*Bufo terrestris americanus*), Spring Peepers (*Acris gryllus crepitans*), Carpenter Frogs (*Rana virgatipes*), Northern Fence Lizards (*Sceloporus undulatus hyacinthinus*), Green Anolis (*Anolis c. carolinensis*), Little Brown Skinks (*Lygosoma laterale*), Florida Green Water Snakes (*Natrix cyclopion floridana*), Northern Water Snakes (*Natrix s. sipedon*), Striped Keelbacks (*Natrix stolata*), DeKay's Snakes (*Storeria d. dekayi*), Red-bellied Snakes (*Storeria o. occipitomaculata*), Eastern Garter Snakes (*Thamnophis s. sirtalis*), Eastern Ground Snakes (*Haldea v. valeriae*), Eastern Ring-necked Snakes (*Diadophis punctatus edwardsi*), Eastern Worm Snakes (*Carphophis a. amoenus*), Black Racers (*Coluber c. constrictor*), Eastern Smooth Green Snakes (*Opheodrys v. vernalis*), Eastern Milk Snakes (*Lampropeltis doliata triangulum*), Florida Crowned Snakes (*Tantilla coronata wagneri*), Northern Copperheads (*Ancistrodon contortrix mokeson*), baby House Mice (*Mus musculus*), baby white mice and strips of horse meat.

All of these items were offered in an unaltered condition, and many of them were also rubbed with live and dead Asiatic snakes and lizards of several species not recorded. Several of the young were force-fed with some of the above-listed food animals and with a prepared liquid food mixture.

Summary

Two King Cobras (*Ophiophagus hannah* Cantor) from near Bangkok, Thailand, have mated during two successive years in the New York Zoological Park. Observations are reported on their courtship and mating. Three matings were recorded in 1955 and six in 1956. Five to six weeks after the last mating in each year the female constructed a large nest of bamboo stalks, bamboo leaves and magnolia leaves. On April 24 of each year she deposited her eggs, 41 the first year and 51 the second. A high percentage of each clutch consisted of abortive eggs. The female remained on the nest guarding the eggs until all had been removed. Young hatched ten to eleven weeks after the eggs were laid, but refused all food offered and lived only four to five months.

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EXPLANATION OF THE PLATES

(Note that in the photographs the neck of the female is sometimes inflated in an abnormal fashion. This is apparently a recurrent condition in this specimen). All photographs by Staff Photographer Sam Dunton.

Plate I

Fig. 1. The courting pair crawl slowly around the cage, with the male on top of the female. The water pool and planting area are at extreme left; the shift cage door is visible on the right.

Fig. 2. The heads and the anterior bodies of the courting pair. (Enlarged from a 16 mm. motion picture film).

Fig. 3 The male frequently flicks his tongue on the head of the female. (Enlarged from a 16 mm. motion picture film).

Plate II

Fig. 4. The male (upper) prods the female (lower) at the start of courtship. They are on a pile of bamboo leaves in a corner of the cage. Note vertical bamboo sticks. (Enlarged from a 16 mm. motion picture film).

Fig. 5. The posterior parts of the bodies showing how the male (right) places his tail under the female's tail at the moment the hemipenis is inserted. (Enlarged from a 16 mm. motion picture film).

Plate III

Fig. 6. The female (foreground) and the male (rear left) in copulation, approximately thirty minutes after the beginning of the mating. This picture shows almost the entire cage in which the snakes were kept. The water pool is in the left foreground and the main door to the cage in the left background.

Fig. 7. The female looping her body around some bamboo leaves and sticks preparatory to pulling them into the nest pile at the beginning of nest building. The site of the nest is behind the vertical sticks of bamboo in the right background.

Plate IV

Fig. 8. The female beginning to draw in a clump of magnolia leaves. Seen from above with nest site at right rear behind vertical bamboo sticks.

Fig. 9. The female coiled on her eggs at the conclusion of laying, April 24, 1955.

Fig. 10. The exposed egg cluster deposited on April 24, 1956. These were in second nest built in 1956 and forward from site of previous nest.

Plate V

Fig. 11. Five eggs and two hatchling King Cobras.

Fig. 12. A hatchling King Cobra spreading its hood in a defensive posture before fully emerged from the egg.

FIG. 1

FIG. 2

FIG. 3

REPRODUCTION IN THE KING COBRA, OPHIOPHAGUS HANNAH CANTOR

FIG. 4

FIG. 5

REPRODUCTION IN THE KING COBRA, OPHIOPHAGUS HANNAH CANTOR

FIG. 6

FIG. 7

REPRODUCTION IN THE KING COBRA, OPHIOPHAGUS HANNAH CANTOR

FIG. 8

FIG. 9

FIG. 10

REPRODUCTION IN THE KING COBRA, OPHIOPHAGUS HANNAH CANTOR

FIG. 11

FIG. 12

REPRODUCTION IN THE KING COBRA, OPHIOPHAGUS HANNAH CANTOR

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An Intricate Genetic System that Controls Nine Pigment Cell Patterns in the Platyfish

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(Plate I; Text-figure 1)

THE genetic theory to account for the initiation and development of melanomas in platyfish-swordtail hybrids states that one principal gene, which controls the normal growth of large black pigment cells in the platyfish, interacts with a number of growth-modifying genes of the swordtail; as a consequence, the melanocytes, which normally would develop into macromelanophores, do not mature but retain their generalized juvenile characteristics and, as neotenous cells, the melanocytes accumulate, proliferate and eventually produce the melanoma in the hybrid organism (Gordon, in press).

One of the practical consequences of this theory is that it explains how it is possible for two normal parents (each representing a stock in which cancer has never been known) to have offspring in which cancer will develop in response to purely hereditary factors. The fortuitous combination of some primary gene for a specific cell and its growth-modifying genes may account for some puzzling manifestations of normal as well as atypical cell growth.

In view of the important role of gene modifiers (genes which have no apparent visible effect when present alone but which may have a profound effect when they are associated with an appropriate primary gene), it is valuable to have additional evidence of their specific genetic activities. The genetic reaction which will be described produces no atypical growth, but it establishes more firmly than before that some genes are capable of modifying the usual pattern of pigment cell growth. This paper is concerned with the transformation, through gene action, of one pigmentary pattern known as the *twin-spot* into another called the *Guatemala-crescent.*

In an examination of 5,019 sexually mature platyfish, *Xiphophorus maculatus,* that represented four natural populations from Mexico and Guatemala, Gordon (1947) detected only two specimens, both collected in 1931 from Lago de Petén, Guatemala, that had a unique color pattern which he called the *Guatemala-crescent.* He gave the rare pattern the genetic symbol of *Cg* to distinguish it from each of seven other common, hereditary patterns which some platyfish have at, or near, the caudal fin. He pointed out that the *Guatemala-crescent* closely resembled the *single crescent, C,* pattern but that *Cg* was "broader overall and particularly so at the ends of the crescent."

Additional collections of the platyfish from four other rivers in southern Mexico and British Honduras have now swelled the total number of adult platyfish examined to more than 9,000, and yet no other fish with the *Guatemala-crescent* pattern was found under natural conditions (Gordon & Gordon, in press). Several years ago, however, the author did find some live platyfish with the *Cg* pattern that were being maintained by a New York aquarist.

It is most unlikely that the aquarium-bred platyfish with the *Guatemala-crescent* pattern are traceable to the natural population of platyfish from the Lago de Petén, a location which is, and has been, inaccessible to the commercial aquarium fish collector. Gordon (1954) suggested that the earliest shipment of platyfish from "Central America" to Europe, in 1907, consisted of a few specimens that were most

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probably collected in the vicinity of Belize in British Honduras.

In a preliminary statement on the problem, Gordon (1951) had suggested that the *Guatemala-crescent* pattern may be referred to the complementary action of two dominant genes, one a primary allele, *T*, for *twin-spot*, which produces two discrete groups of small pigment cells near the tail fin, and a complementary gene, *Cg; Cg* produces no visible expression by itself, but in combination with *T* it acts to bring an additional number of small pigment cells to the area between the two discrete groups of micromelanophores. The result is that a crescent-like bridge of pigment cells is formed that unites the two outer dark clusters; the whole effect is then categorized as the *Guatemala-crescent*, Plate I, Fig. 1.

The Genetic Results

The general method of inheritance of the *Guatemala-crescent* pattern was demonstrated in the offspring of the mating of a purchased female platyfish having a *Guatemala-crescent* to a double recessive. From the results in the F_1, the P_1 were of the genetic constitution set forth in Table 1.

In another and apparently similar mating, slightly different results were obtained which indicated that the parents in the second mating were of the following genetic constitution:

Female		Male
T Cg/+ +	×	+ +/+ +

Phenotypes in F_1	Observed	Expected
1. *Guatemala-crescent, T Cg*	6	5.5
2. *Twin-spot, T*	6	5.5
3. No tail patterns, +	10	11.0

Autosomal or Sex-linked

The determination of whether the modifier *Cg* is sex-linked or autosomal was accomplished, in part, from a mating involving the dominant, sex-linked gene, *Sp*, for generalized black (macromelanophore) spotting on the body. A black-spotted female, (W) + (Y) *Sp*, was mated with a male that was recessive for the sex-linked gene, (Y) + (Y) +, but dominant for the *twin-spot* gene, *T*. The results in the F_1 were as shown in Table 2.

The criss-cross inheritance of the sex-linked *Sp* gene from the mother to her sons is characteristic of the domesticated strain of the platyfish in which the female is WY, the male YY, (Gordon, 1931); the *Sp* gene was presumably carried on the Y chromosome of the P_1 female. The *Cg* gene must have been carried by the *Sp* female parent because the male parent had the *twin-spot, T*, pattern only. The *Cg* gene, since it appeared in both sexes among the F_1, could not have been sex-linked. These results in addition to those obtained from the first mating, in which the female parent carried *Cg*, indicate that *Cg* is autosomal in its inheritance.

Test for Linkage to the Autosomal Gene *St* (+)

The inheritance of *Cg* was studied in association with a previously determined dominant, autosomal gene for *stippling, St* (Gordon, 1937). The gray color that the *St* gene produces, by a show of many micromelanophores, contrasts sharply with *golden*, which is its recessive effect. The P_1 were as shown in Table 3.

The results favor the conclusion that *Cg* is inherited independently of the *stipple* gene (*St*, +). Although the data are few, indeed, they indicate that if *Cg* were linked completely to *St* in the *Stippled* parent (*Cg St*) no *Stippled, Twin-spot* (*T* + *St*) F_1 should have appeared, yet nine did. If *Cg* were completely linked to the recessive + of the *Stippled* gene in the *Stippled* parent, *Cg* +, then no *Golden, Twin-spots* (*T* + +) F_1 should have appeared, yet four did.

While *Cg* and *T* appear in the expected ratios, the stippled fish outnumber the golden disproportionately. This has been observed and discussed by the author in previous papers but it is not pertinent to the study of the *T Cg* reaction.

Tests with Alleles, *Cc, C* and *O*

In the next series of experiments, the possible effects of *Cg* were tested on some of the other alleles of *T*, such as *Cc* for *complete-crescent, C* for *single crescent, O* for *one-spot* and *Co* for *comet* (Gordon, 1947).

1. Test with *Cc*, Complete-crescent

In order to determine whether *Cg* had any visible effect on the *complete-crescent* pattern, the genes *Cc* and *Cg* were combined in the following manner:

Guatemala-crescent		*Complete-crescent*
T Cg/+ +	×	*Cc* +/+ +

F_1 Phenotypes	Observed	Expected
1. *Complete-crescent, Guatemala-crescent, TCc Cg*	14	14.5
2. *Complete-crescent, Twin-spot, TCc*	7	14.5
3. *Complete-crescent, Cc*	35	29.0
4. *Guatemala-crescent, T Cg*	11	14.5
5. *Twin-spot, T*	16	14.5
6. No tail patterns, +	35	29.0
Totals	118	116.0

In counting the various F_1 phenotypes, the *complete-crescent, Cc,* pattern was identifiable in combination with the overlapping *T* and *T Cg* patterns, owing to the unobscured wedge-shaped mark of *Cc,* which is outside the range of *T* and *T Cg.*

In a follow-up experiment, the complete segregation of *T* from *Cc,* in the presence of *Cg,* was demonstrated by mating a platyfish with both a *complete-crescent* and a *Guatemala-crescent* back to one without a tail pattern as follows:

Complete-crescent, Guatemala-crescent		No Pattern
T Cg/Cc +	×	*+ Cg/+ Cg*

F_1 Phenotypes	Observed	Expected
Guatemala-crescent, T Cg	12	11
Complete-crescent, Cc	10	11

2. Test with Single Crescent

In order to determine whether *Cg* has any effect on the *single-crescent* gene, *C,* a platyfish with a *Guatemala-crescent* was mated to one with the *C* pattern. Results are seen in Table 4.

The expected frequencies given above are based upon two assumptions. First, that the genotypes of the parents were one or the other of the following:

Guatemala-crescent	×	*Single-crescent*
1. *T Cg/+ Cg*		*C +/+ +*
2. *T Cg/+ +*		*C Cg/+ Cg*

The second assumption is that when *C* is present in combination with *T Cg* the *single-crescent* pattern is completely obscured; *C* is not changed, and, certainly, *C* is not extended.

3. Test with One-spot

The ineffectiveness of the modifier *Cg* in changing the phenotypic expression of the *O*

Table 1.

Female *T Cg/T +* × Male *+ +/+ +*

Phenotypes in F_1	Female	Male	Observed	Expected
1. *Guatemala-crescent, T Cg*	11	7	18	21.5
2. *Twin-spot, T*	16	9	25	21.5

Table 2.

	Females		Males	
Phenotypes in F_1	Observed	Expected	Observed	Expected
1. *Spotted, Guatemala-crescent, Sp T Cg*	0	0	7	7
2. *Spotted, Twin-spot, Sp T*	0	0	7	7
3. *Guatemala-crescent, T Cg*	6	7	0	0
4. *Twin-spot, T*	8	7	0	0

Table 3.

Golden, Guatemala-crescent T Cg +/+ + + × *Stippled + Cg St/+ + +*

			Expected if linked	
F_1 Phenotypes	Observed	No linkage	*Cg St*	*Cg +*
1. *Stippled, Guatemala-crescent, T Cg St*	23	18	24	12
2. *Stippled, Twin-spot, T + St*	9	6	0	12
3. *Stippled, + St*	29	24	24	24
4. *Golden, Guatemala-crescent, T Cg +*	14	18	12	24
5. *Golden, Twin-spot, T + +*	4	6	12	0
6. *Golden, + +*	16	24	12	24
	—	—	—	—
	95	96	96	96

Table 4.

Phenotypes in F_1	Presumed Genotypes	Observed	Expected
1. *Guatemala-crescent*	*T Cg/C +* or *T Cg/+ +*	10	12.5
2. *Single-crescent*	*+ Cg/C +*	7	6.25
3. No tail pattern	*+ Cg/+ +*	8	6.25

allele for *one-spot* was clearly demonstrated in three matings.

1. *O +/Cc +* × *T Cg/+ +*

F_1 Phenotypes	Observed	Expected
1. *One-spot, Guatemala-crescent, OT Cg*	6	7.5
2. *One-spot, twin-spot, OT*	9	7.5
3. *One-spot only, O*	19	15.0
4. *Crescent-complete, Guatemala-crescent, CcT Cg*	6	7.5
5. *Crescent-complete, twin-spot, CcT*	5	7.5
6. *Crescent-complete, Cc*	15	15.0

The 19 *one-spots* were not modified in appearance.

2. *O +/T +* × *Cc +/T Cg*

F_1 Phenotypes	Observed	Expected
1. *OT Cg*	7	6
2. *OT*	2	6
3. *OCc*	10	12
4. *CcT Cg*	8	6
5. *CcT*	8	6
6. *TT Cg*	6	6
7. *TT*	7	6

The *one-spot, O,* pattern was not modified in any of the three phenotypes in which it appeared.

3. The third mating involves, in addition to *O, T* and *Cg,* the independent autosomal gene *St* for the stippling effect of many micromelanophores which cover the entire body; the recessive (*stst*) effect is *golden* since most micromelanophores are lacking. One parent had *stipple, St, one-spot, O,* and *twin-spot, T;* the other was *golden* without tail markings, + + +. From the results of the mating it was demonstrated that the *golden* parent had been homozygous dominant for the *Cg* modifier.

O + St/T + + × *+ Cg +/+ Cg +*

F_1 Phenotypes	Observed	Expected
1. *Stippled, One-spot, O Cg St*	21	17.5
2. *Golden, One-spot, O Cg*	16	17.5
3. *Stippled, Guatemala-crescent, T Cg St*	16	17.5
4. *Golden, Guatemala-crescent, T Cg*	17	17.5

Separation of *Cg* from the Modifier *E*

The testing of the effect of *Cg* on the *comet, Co,* allele was complicated because the expression of *Co* is radically extended and changed by its own specific modifier *E.* Gordon (1946) showed that the combination *Co E* produces the *wagtail* pattern, in which all the fins and extremities are blackened by small black pigment cells. The question that needed clarification was whether the modifier *E* was synonymous with *Cg,* or whether there were, as originally suspected, two independent genetic modifiers, *E* that acts on *Co* and *Cg* that acts on *T.*

In two matings, a platyfish with *Co* and *T* was mated to a melanin-free, albino swordtail, *X. helleri,* because it was previously established by Gordon (1946) that many swordtails carry the modifier *E.* The following results were obtained in the F_1:

Phenotypes F_1	
1. *Wagtails, Co E*	26
2. *Guatemala-crescents, T Cg*	18

From the above results it was not clear whether there were one or two gene modifiers.

In some measure the distinctness of *Cg* was demonstrated by the results of mating a *comet* platyfish with one having a *twin-spot* pattern. The presumed genotypes of the P_1 were:

Comet *Twin-spot*

Co +/+ + × *T E/+ +*

F_1 Phenotypes	Genotypes	Observed	Expected
1. *Wagtail*	*Co E/T +*	3	3.50
Wagtail	*Co E/+ +*		
2. *Comet, twin*	*Co +/T +*	2	1.75
3. *Comet*	*Co +/+ +*	2	1.75
4. *Twin-spot*	*T E/+ +*	3	3.50
Twin-spot	*T +/+ +*		
5. No pattern	*+ E/+ +*	4	3.50
No pattern	*+ +/+ +*		
		14	14.0

The significant fact is that 3 of the 14 offspring had the *wagtail* pattern. This meant that the *E* modifier was carried by the *T* parent but that it had had no effect on the expression of *T.* Phenotypically, *Co E T* and *Co E* look alike and must be classified as *wagtails.*

In another mating a reverse effect was obtained, namely, the *comet* parent was harboring the *Cg* modifier. This was revealed when a *comet* was mated with a *twin-spot* platy as is indicated in Table 5.

While the matings involving *Co* and *T* yielded relatively few individuals, the very existence and recognition of some of the combinations support the conclusion that there are two specific modifiers, *E* and *Cg,* each of which reacts with its own specific primary gene, *Co* and *T,* respectively. For example, the combination of *Co Cg/T +* appeared four times in the last mating. If *Cg* modified *Co* as well as *T,* these four would have appeared as *wagtails,* but actually the patterns in the four were clearly recognized as being *comet* and *Guatemala-crescent;* there were no *wagtails* at all, Plate I, Fig. 2.

In order to get more evidence of this sort, another experiment was performed with similar phenotypes, that is, a *comet* platyfish was mated with a *twin-spot* as shown in Table 6.

In the F_1, 18 *comet, Guatemala-crescent* platyfish were observed, showing that the *Co* is not modified by the *Cg* gene. When one of the *Co Cg/T* + (*Comet, Guatemala-crescent*) F_1 platyfish was backcrossed to a platyfish that lacked a tail pattern, the results indicated that the parents must have had the genotypes set forth in Table 7.

No *twin-spot* patterns appeared among the F_1. From these results, it is clear that *Cg* has no visible effect on *Co* but rather that its action is restricted to the modification of *T*.

Presence of *Cg* in a Related Species

In a previous study of the modifier *E*, Gordon (1946) showed that this gene is found frequently in the swordtail, a close relative of the platyfish. In order to determine whether the swordtail, *Xiphophorus helleri*, carries the *Cg* gene, a *twin-spot* platyfish from a commercial stock was mated to a swordtail that belonged to a stock originally obtained from the Río Papaloapan in Mexico.

Twin-spot Platyfish		Plain Swordtail
T+/+ +	×	+ *Cg*/+ *Cg*

F_1 Phenotypes	
1. *Guatemala-crescent, T Cg*	35
2. No tail patterns, *Cg*	32

Since about 50% of the platyfish-swordtail hybrids showed the *Guatemala-crescent* and half showed no peduncular marking, the swordtail must have been homozygous for the modifier *Cg*. This indicates that some swordtails taken from natural habitats harbor a gene which apparently has no visible effect upon the members of its own species but which is capable of interacting with a specific gene of a different species, Plate I, Figs. 3 & 4.

Discussion

The data presented in this paper support the

Table 5.

Comet Co Cg/+ + × *Twin-spot T* +/+ +

F_1 Phenotypes	Genotypes	Observed	Expected
1. *Comet, Guatemala-crescent*	*Co Cg/T* +	4	1.5
2. *Comet, twin-spot*	*Co* +/*T* +	0	1.5
3. *Comet*	*Co Cg*/+ +	3	3.0
Comet	*Co* +/+ +		
4. *Guatemala-crescent*	*T Cg*/+ +	1	1.5
5. *Twin-spot*	*T* +/+ +	1	1.5
6. No pattern	+ *Cg*/+ +	3	3.0
No pattern	+ +/+ +		
		12	12.0

Table 6.

Comet *Co Cg*/+ + × *Twin-spot* *T* +/*T* +

F_1 Phenotypes	Genotypes	Observed	Expected
1. *Comet, Guatemala-crescent*	*Co Cg/T* +	18	23
2. *Comet, twin-spot*	*Co* +/*T* +	23	23
3. *Guatemala-crescent*	+ *Cg/T* +	32	23
4. *Twin-spot*	+ +/*T* +	19	23
		92	92

Table 7.

Comet, Guatemala-crescent *Co Cg/T* + × No Pattern + *Cg*/+ *Cg*

Phenotypes in F_1	Genotypes	Observed	Expected
1. *Comet* only	*Co Cg*/+ *Cg*; *Co Cg*/+ +	14	15
2. *Guatemala-crescent*	*T Cg*/+ *Cg*; *T Cg*/+ +	16	15
		30	30

conclusion that in platyfish the *Cg* gene is a specific autosomal modifier of the *twin-spot* gene, *T; Cg* is not linked to *E*, which is a specific modifier of *comet, Co*. Nevertheless *T* and *Co* are alleles; both belong to a common series of seven dominant multiple alleles (Gordon, 1947). These facts reveal the existence of an intricate and interlocking genetic system for the production of nine distinctive patterns, all of which may appear only at the posterior region of the platyfish, and all of which are composed of a specific type of pigment cell, the micromelanophore. This interlocking and precise genetic system depends not only upon seven multiple alleles (plus one universal recessive), but also upon two independently inherited specific gene modifiers. In graphic form, the genetic system is represented by Text-fig. 1.

1. Frequency of the *Cg* Gene in Natural Populations

The frequency of the *Cg* gene modifier in the upper Río Usumacinta and the Lago de Petén area may be estimated on the basis of the frequency of the *T* allele; because only when the *T* allele is present can the presence of the *Cg* gene be detected. Gordon (1947) found that of 552 adult platyfish, which represented the entire Guatemala collection made in 1935, 31 specimens had the *T* allele either alone (13) or in combination with other members of its allelic series (18). In 2 of the 31, the *T* allele was modified by the *Cg* gene to produce the *Guatemala-crescent* pattern. The presence of the *Cg* gene on the basis of the 31 *twin-spot* platyfish is therefore 6.4%. In contrast, the presence of the *T* allele on the basis of 31 platyfish out of 552 is 5.6%. Thus, it would appear that the frequency of the *Cg* gene in the Río Usumacinta population as a whole is slightly greater than the frequency of the *T* allele it modifies. Actually, however, the frequency of the *Cg* gene might better be calculated from the limited number of platyfish from the Lago de Petén basin because the modifier *Cg* has been detected only in this area. In the Lago de Petén, which includes Petenxil and Ponteil but excludes Laguna de Zotz (Stations 12 to 20, Gordon, 1947), 79 platyfish were collected of which 14 had the *T* allele, the gene frequency of *T* in the platyfish from the Lago de Petén basin is 0.093, and of *Cg* 0.074; both calculated by the usual formula $f = 1 - \sqrt{1-p}$.

The distribution of the *Cg* gene is restricted not only in the platyfish of Guatemala, but it is probably non-existent among all the other known natural populations of the platyfish. For example, Gordon & Gordon (in press) evaluated the frequencies of the *twin-spot* and six other tail patterns among the platyfish of eight large river populations. To attain maximum accuracy, they based their evaluation on the frequencies of *single* tail patterns only; double patterns were deliberately excluded because many of them were difficult to identify with complete assurance. The frequencies of the single *twin-spot* patterns in each of eight natural populations of the platyfish were as follows:

	Number of Platyfish	Single *Twin-spots*	%
1. Jamapa	860	54	6.3
2. Papaloapan	3,492	138	4.0
3. Coatzacoalcos	1,334	252	18.9
4. Tonala	178	5	2.3
5. Grijalva	651	50	7.7
6. Usumacinta	552	13	2.4
7. Hondo	327	10	3.1
8. Belize	1,526	78	5.1

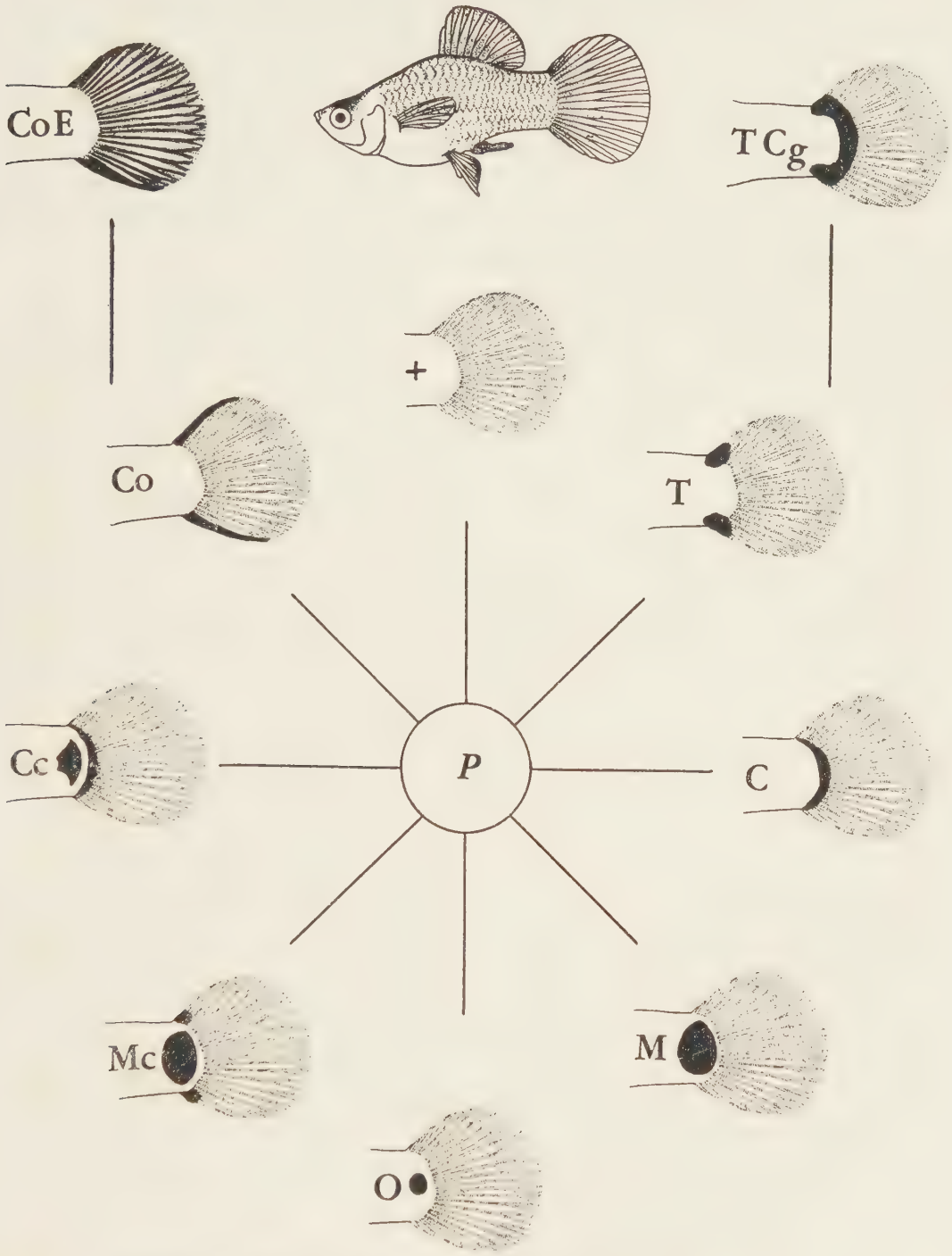
On the basis of this sample of Gordon & Gordon's (in press) data, it is evident that the *Cg* gene is either lacking in the eight river populations (except in Lago de Petén) or it is extremely rare. While the platyfish of the Lago de Petén have been assigned to the Río Usumacinta population, this analysis points up the fact that a local population within an assigned river system may differ genetically from its other local populations.

2. Introgression of the *Cg* Gene from One Species to Another

With regard to the mechanism of inheritance of the *Cg* gene in the platyfish, it is exactly similar to that of an equivalent color pattern of the domesticated swordtail which was previously analyzed by Kerrigan (1934) and confirmed by Gordon (1937). The genetic symbols these authors used varied, however:

	Xiphophorus maculatus	*Xiphophorus helleri*	
Phenotype	Gordon (in press)	Kerrigan (1934)	Gordon (1937)
Guatemala-crescent	*T Cg*	*C P*	*C P*
Twin-spot	*T* +	*C p*	*T P*
No pattern	+ *Cg*	*c P*	*C p*
No pattern	+ +	*c p*	*T p*

It seems strange that the inheritance of the *twin-spot* and *Guatemala-crescent* patterns should have been worked out first in the swordtail, because *X. helleri* in its many native habitats does not have any of these patterns. Aquarium-reared swordtails, however, obtained the *T* gene from the platyfish about 1911 by experimental introgressive hybridization made



TEXT-FIG. 1. Nine Pigment Cell Patterns. The intricate genetic system that controls nine specific pigment cell patterns in the platyfish, *Xiphophorus maculatus*, is built around the central gene *P* for seven melanic patterns located in the anterior part of the caudal fin and the posterior part of the caudal peduncle. The gene *P* has a series of seven dominant, autosomal, multiple alleles: *PT*, *PC*, *PM*, *PO*, *PMc*, *PCc*, *PCo* plus the multiple recessive *P+*. For convenience the symbol *P* is deleted from the formulae for the patterns which are written *T* for *PT*, etc.

Superimposed upon the *P* series of alleles are two independent, autosomal gene modifiers: *Cg* that interacts specifically with *T*, and *E* that interacts exclusively with *Co*. Neither *Cg* nor *E* have any visible expression by themselves, nor any visible effect upon the *P* multiple alleles other than *T* and *Co*.

T = *Twin-spot* *C* = *Crescent* *O* = *One-spot* *Co E* = *Wagtail complex* *Mc* = *Moon-complete*
Co = *Comet* *M* = *Moon* *T Cg* = *Guatemala-crescent* *Cc* = *Complete-crescent* + = No tail pattern

possible by the selective breeding and hybridization trials of German aquarists. When in 1911 the *twin-spotted* swordtails were sent by German aquarists to the British Museum (Natural History) for identification, Regan (1911) at first regarded the *Xiphophorus* with the *twin-spot* as a new species and named it *rachovii* on the assumption that it had been collected at Puerto Barrios, Guatemala. Later, when Regan (1913) obtained swordtails unquestionably from Puerto Barrios, he saw that the fish did not have any markings resembling the *twin-spot* or *crescent*. Consequently he suspected that the *"rachovii"* type was of hybrid origin, produced in the aquarium. He therefore recommended that the name *Xiphophorus rachovii* be regarded as invalid. As indicated in the present paper, a *twin-spot* platyfish mated with a swordtail produced a hybrid that had the *Guatemala-crescent* pattern. This confirms Regan's suggestion that *X. rachovii* was a fish of hybrid origin, Plate I, Figs. 5 & 6.

Once the *Guatemala-crescent* pattern was synthesized by fish fanciers in the platyfish-swordtail hybrids, some breeders, by backcrossing *T Cg* hybrids to platyfish, recreated the platyfish body type and distinguished it by the *T Cg* color pattern. Thus, while the aquarium-bred *"rachovii"* swordtails owe their color pattern to the *T* gene of the platyfish, the color pattern in the aquarium-bred *Guatemala-crescent* platyfish is traceable to the *Cg* gene of the swordtail. The development of *Guatemala-crescent* patterns in two related species of fishes illustrates an example of what may be called *reciprocal introgression.*

While precise data on the frequency of the *Cg* gene in the swordtail are not available, it would appear from the experiences of fish fanciers that the frequency of *Cg* is probably much higher in wild *X. helleri* than in wild *X. maculatus.* Just what function *Cg* serves in contemporary swordtails is unknown since, as is the case in the platyfish, *Cg* has no visible effect in the absence of the *T* gene. Perhaps in the early evolution of the xiphophorin fishes, *Cg* imparted some advantage to their members and was by this virtue retained in some of the present day species. It is odd, however, that the *Cg* gene, as far as can be determined, is restricted to a few local populations of *X. maculatus* within a small part of the Lago de Petén basin of Guatemala. This represents a tiny area considering the wide range of *X. maculatus,* which extends southeast from the Río Jamapa, near the city of Veracruz, Mexico, across southern Yucatan peninsula to the Belize River, near the city of Belize in British Honduras.

The discovery of the action of the *Cg* gene in the platyfish has cleared up the problem of the "rarity" of the *Guatemala-crescent* pattern, but it does not explain the significance of the gene's survival in only one of its many geographical races, nor its probable higher frequencies among races of swordtails.

Summary

A specific gene, *Cg,* was found to modify the *T* (*twin-spot*) allele which is one of seven multiple alleles of the *P* gene for seven pigmentary patterns in the platyfish. The combination of *T Cg* produces the *Guatemala-crescent* pattern which has been observed only twice in more than 9,000 adult specimens taken from eight natural populations of the platyfish. The distribution of *Cg,* under natural conditions, is restricted solely to the Lago de Petén area of Guatemala. There its frequency is not rare, for it approaches that of the *T* allele.

Previously, another gene modifier *E* was found to interact specifically with the *Co* (*comet*) allele of the *P* gene to produce the *wagtail* complex, *Co E.* Thus, on the basis of seven multiple alleles of the *P* gene and two independent gene modifiers, nine patterns are produced. Neither modifier *Cg* nor *E* alone has any visible effect in the platyfish or in the swordtail.

By introgressive hybridization, the genes *T* and *Co* have been transferred to swordtails under domestication to produce the *Guatemala-crescent* and *wagtail* swordtails. In a reverse direction aquarium-bred *Guatemala-crescent* and *wagtail* platyfish have obtained the gene modifiers *Cg* and *E* from the swordtail. Thus, the *Guatemala-crescent* and the *wagtail* platyfish and swordtails represent an example of reciprocal introgression.

These experiments show how it is possible for two parents, from stocks which never had a *Guatemala-crescent* or a *wagtail* pigmentary pattern, to have offspring in which one or the other of these patterns will appear. The results demonstrate the reality of specific gene modifiers.

Acknowledgements

I thank Pamela Alexander and James W. Atz for reading the manuscript and Sam C. Dunton for the first four photographs in Plate I.

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EXPLANATION OF THE PLATES

Plate I

Fig. 1. A platyfish, *Xiphophorus maculatus,* with a *twin-spot* (*T*) pattern is at the left. The one to the right has a *Guatemala-crescent* (*T Cg*) pattern; note that the *T Cg* complex also involves dot-like markings at the mandibular junction.

Fig. 2. The male platyfish, *Xiphophorus maculatus,* (to the left) has no tail pattern. The female (to the right) has *comet* (*Co*) and *Guatemala-crescent* (*T Cg*) patterns; note the small black dot at the mandibular junction in the female.

Fig. 3. The male platyfish, *Xiphophorus maculatus,* shown in the upper left, having a *comet, Co,* and *twin-spot, T,* pattern, was mated to a female albino swordtail, *X. helleri,* shown in the lower right. Their F_1 hybrids are shown in Fig. 4.

Fig. 4. The first-generation platyfish-swordtail hybrids; the one on the left shows the wagtail complex, *Co E*; the one on the right shows the *Guatemala-crescent* pattern, *T Cg*.

Figs. 5 & 6. The so-called *"rachovii"* swordtails are actually hybrids reconstructed to look like swordtails. These "swordtails" have been produced by fish culturists by a series of backcrosses of the hybrids to swordtails; that is, by introgressive hybridization. The female swordtail, Fig. 5, shows just the effects of the *T* gene. The *Guatemala-crescent* pattern which characterizes the male, Fig. 6, is traceable to the *T* gene of the platyfish and the *Cg* gene of the swordtail.

FIG. 1

FIG. 2

FIG. 3

FIG. 4

FIG. 5

FIG. 6

AN INTRICATE GENETIC SYSTEM THAT CONTROLS NINE PIGMENT CELL PATTERNS IN THE PLATYFISH

19

Introduced Mammals and Their Influence on Native Biota[1]

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(Text-figure 1)

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INTRODUCTION

IT is characteristic of man to alter his environment, and he has attempted in various ways to improve upon the conditions of nature. Unfortunately some attempts, such as indiscriminate deforestation and draining of swamps, have had bad effects. The ruthless extermination of many forms of plants and animals, or their uncontrolled introduction into new environments, also fall into this category.

In recent years the faulty reasoning behind the introduction of animals has become increasingly apparent. Biologists now are generally opposing the liberation of exotics into the wild, because of the unpredictable nature and possibly unfavorable economic consequences of such action, and because of an aesthetic objection to mixing diverse faunas. In compiling the present data on introduced mammals our aim is to elucidate the results of this practice and to clarify certain principles involved.

Introductions may be classified as intentional or unintentional. Prior to and during the early stages of colonization of many parts of the world, most exotics were imported unintentionally, as "chance" introductions, for example as stowaways on ships. Intentional introductions, for the purpose of establishing foreign species in a new territory, reached a peak during the Nineteenth Century. This paper deals mainly with the intentional introduction of wild mammals. Some information is presented concerning feral mammals, but introduced domestic species are not discussed.

Although the majority of introductions of mammals have failed, most of those which succeeded have proved detrimental to man's interests; only a few have been advantageous. The most serious problem is that of predicting the consequences of an introduction. The exotic only rarely will occupy the niche which the introducer expects it to fill.

The expense involved in introducing a species and getting it established is usually very high and has proved to be a poor investment in most cases. From the economic viewpoint, it is often more practical to foster an increase of native mammals as a means of attaining the desired results.

By and large, it seems impossible to introduce animals under "scientifically controlled" conditions, because of our lack of knowledge of ecologic conditions. There is an obvious need for more detailed research here. Preferably, introductions should be undertaken only after they are carefully studied and approved by an international board of scientists, for too often exotics have not only become a nuisance in the country to which they were introduced, but also in ad-

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jacent countries where they spread as a "gift."

Overly successful introductions usually lead to a demand for control. This is a complex problem, and it is practically impossible or extremely costly to exterminate introduced species which have become well established.

We have attempted to assemble such data as are available on the introduction of alien species of mammals throughout the world, with a more detailed discussion of the consequences of such introductions in the case of certain conspicuous or economically important species. Our efforts have been more fruitful in certain groups and areas than in others. Orders best represented among introduced mammals are the Lagomorpha, Rodentia, Carnivora and Artiodactyla. Although it appears to be impossible to gather a complete record of all mammals which have been introduced or transplanted during historic time, a fairly good picture has been obtained of what has happened in the more recent past.

The subspecific identity of all forms could not be ascertained but this is presented when known. Space limitations do not permit the inclusion of all known cases of transplantations from one point to another within one continental area, as of deer, elk, rabbits and squirrels in North America.

The scientific and common names follow Ellerman & Morrison-Scott (1951), Miller & Kellogg (1955), Laurie & Hill (1954) and Troughton (1947). Where there is doubt as to the name of the animal in question, that given in the original publication is indicated.

The bibliography, although certainly not exhaustive, is intended as a helpful starting point for investigators interested in geographic areas or groups of mammals. The section on North America was prepared by Manville, that on South America by Van Gelder, and most of the balance by the senior author.

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Intentional Introductions or Transplantations

Eurasia:

Introductions of mammals generally seem to have been less successful in Eurasia than on the other continents. This is the largest land mass and has more species of mammals than the New World. Competition there may be more severe, resulting in less chance of success for exotics. Because most emigrations of the white man have been *from* Eurasia, and because he is mainly responsible for recent animal introductions, the number of alien mammals released *in* Eurasia has been less than in other continents.

No data could be obtained for several countries in southeast Asia, and relatively few for the Soviet Union and China. It seems, however, that in the U.S.S.R. introductions and transplantations of fur-bearers have been accomplished on a large scale. From 1929 to 1948, in more than 500 areas inside the boundaries of the Soviet Union, no less than 21 species of fur-bearers, amounting to about 80,000 individuals, apparently were released (Schmidt, 1954). Another source (Naumoff, 1950) states that from 1925 to 1948 more than 115,000 mammals, of 32 species, were released in the Soviet Union.

Table 1 summarizes the introductions and transplantations in Eurasia.

The introduction of the Muskrat *(Ondatra zibethicus)* into Eurasia resulted in a serious threat to the local economy by damage to dikes and roadbeds and, conversely, in the addition of a valuable fur-bearer to Russia and Finland. Three females and two males from Alaska were introduced in the neighborhood of Prague by Prince Colleredo-Mannsfeld in 1905. More Muskrats, probably from Canada, were liberated later by the same person.

The spread of the species from this first site of release was rapid. In Bavaria, for example, in 1923 and 1924, the rate of emigration is said to have amounted to 30 to 45 miles yearly. In 1914, nine years after the first planting, the population in Bohemia alone was estimated at two million. In 1933, the colonized territory embraced about 64,000 square miles (Mohr, 1933). From Bohemia the Muskrat spread mainly in a northerly and easterly direction and now occupies most of Czechoslovakia, eastern Germany, Poland and parts of Yugoslavia, Romania and European Russia (Text-fig. 1). A good discussion of the early spread of the Muskrat in Europe is presented by Storer (1937).

In the 1920s several subspecies of Muskrat were introduced into fur farms in France. Muskrats escaped from several of these farms, and by 1933 were established in twelve areas. The first capture in the wild was made in 1930. Five

centers of infestation were in the basins of the Seine and the Somme, four were in eastern France and three others were in the center of southeastern France. An active campaign of destruction and the use of a virus resulted in the extermination of Muskrats in southeastern France (Bourdelle, 1939). Muskrats entered Switzerland from the area of infestation in Alsace, and by 1950 about 800 had been killed.

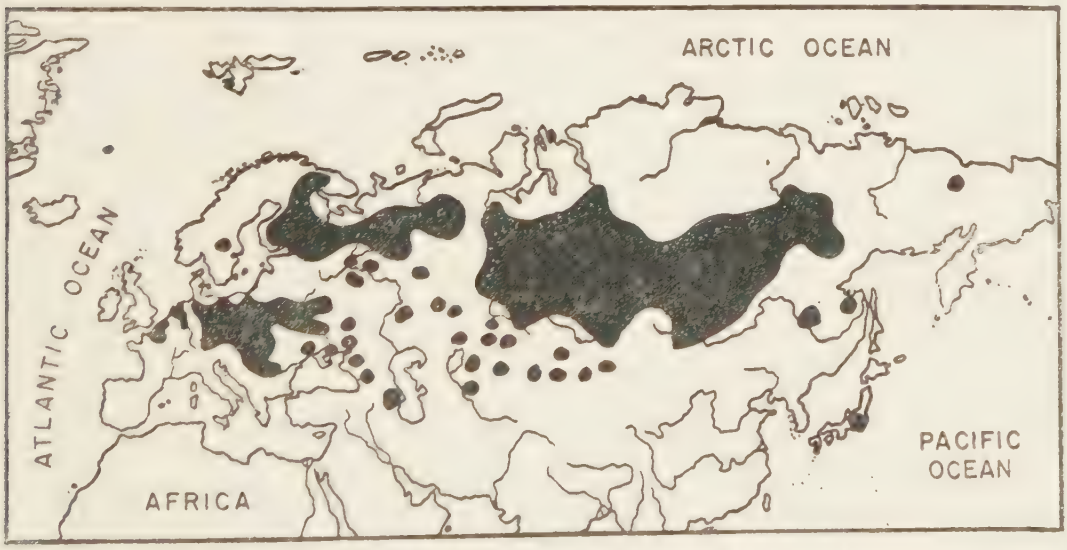
In the Low Countries, the Muskrat occupies nearly all of northern Belgium, as a result of introduction by 1930. In Holland the first Muskrats were caught in 1941, where they are now slowly penetrating along the southern boundary. Government trappers are still keeping the advance in check fairly well (van Koersveld, 1954).

Even before Poland was invaded by the progeny of the Muskrats from Czechoslovakia, some escapees from fur farms had already become established. Nearly all of Poland is now inhabited by the species. The Muskrat was introduced illegally into Sweden sometime before 1944 (Liljeström, 1954). The species was also deliberately introduced at three sites in the lakes region of Finland in 1922 and 1923, from Czechoslovakian stock; other specimens were introduced later from America. They spread from 18 to 25 miles yearly and are now present in most of the country except the extreme north. The Muskrat is now the most important furbearer in Finland, in point of value and of numbers, and 150,000 to 250,000 pelts are harvested annually (Schmidt, 1954; Hoffman, 1952).

The Soviet Union first introduced Muskrats in 1927; from then until 1945, 79,198 were released in the north European and Siberian taiga zone, even as far as Kamchatka, where a shipment arrived from Ontario in 1928 (Eyerdam, 1932). They are still spreading from centers of release (Berger, 1944). In 1941, 150,000 pelts were harvested, and in 1954 about 649,000 (Schmidt, 1954). Nothing specific seems to be known about a supposed introduction into China (Bachrach, 1953). The Muskrat was also introduced in Japan from America, perhaps before 1945; it is confined to Tokyo and environs (Kuroda, 1955).

The only area where the Muskrat has been successfully eradicated is the British Isles. Since 1929 there have existed 87 farms from which animals escaped to establish colonies in England, Scotland and Ireland. Around 1930 it was forbidden to keep Muskrats on fur farms, and a successful system was devised to exterminate them (Warwick, 1934). By 1935, young Muskrats were no longer captured, and by 1939 the campaign was considered terminated; 4,299 animals had been caught.

Only in Finland and Russia is this rodent of value as a fur-bearer, and here no problem of damage seems to exist. In western Europe, however, its burrowing is extremely harmful to dikes, roads and fish-ponds. The freshwater pondfishing industry accuses it of eating fish and damaging nets; also it raids garden crops. Certainly the sums expended on destruction of Muskrats and repairing their damages are much higher than the profits obtained from fur and flesh. It is still doubtful whether further spread of this introduced mammal can be curtailed.



TEXT-FIG. 1. The present distribution of the Muskrat in Eurasia, derived from stock originally introduced from North America (modified after M. Hoffman, 1952).

TABLE 1: MAMMALS INTRODUCED OR TRANSPLANTED IN EURASIA

Common Name	Scientific Name	Year(s) of Liberation	Country or Place of Origin	Country or Place of Introduction	Reason for Introduction
A: *Established; increased in numbers and/or range:*					
1. *From another continent*					
Gray Squirrel	*Sciurus carolinensis*	1890	N. America	British Isles	Pet
Muskrat	*Ondatra zibethicus*	1905	Canada?	Czechoslovakia	Fur
Nutria	*Myocastor coypus*	1930s	S. America	Several countries	Fur farming
American Beaver	*Castor canadensis*	. . .	N. America	Russia	Fur
American Mink	*Mustela vison*	Recent	N. America	Scandinavia, Iceland	Fur farming
Alaskan Fox	*Vulpes fulva alascensis*	Recent	Alaska	Eur. Russia	Fur
American Red Fox	*Vulpes fulva*	Recent	N. America	Eur. Russia	Fur
White-tailed Deer	*Odocoileus virginianus*	1934, 1947	U.S.A.	Finland	Hunting
2. *From the continent to islands or vice versa, or between islands*					
Pig-tailed Macaque	*Macaca nemestrina leonina*	Recent	Burma	Andaman Is.	?
Formosan Macaque	*Macaca cyclopis*	Since 1942	Formosa	Oshima, Japan	Escaped
Crab-eating Macaque	*Macaca irus*	?	Western Indonesia	Celebes, Lesser Sunda Islands	?
Crested Celebes Macaque	*Cynopithecus niger*	?	Western Indonesia	Batchian Is.	?
Black-naped Hare	*Lepus nigricollis*	?	India or Ceylon	Java	Hunting
Golden-backed Squirrel	*Callosciurus caniceps*	1940s	Formosa	Japan	Zool. Gardens
Northern Red-backed Vole	*Clethrionomys rutilus*	1870	Kamchatka	Bering Is.	?
Fat Dormouse	*Glis glis*	1886	Europe	British Isles	?
Javan Mongoose	*Herpestes javanicus*	?	Indonesia	Ambon	?
European Red Fox	*Vulpes vulpes*	Recent	British Isles	Sweden	Fur
Siberian Weasel	*Mustela sibirica coreana*	1930s	Korea	Japan	Fur farming
Siberian Weasel	*Mustela sibirica itatsi*	Before 1901	Japan	Hokkaido	Fur farming, rat control
Ermine	*Mustela erminea*	1931	Holland	Terschelling Is.	Rat control
Weasel	*Mustela nivalis*	1931	Holland	Terschelling Is.	Rat control
Masked Palm Civet	*Paguma* sp?	?	Formosa or China	Japan	Cage animal
Malay Civet	*Viverra tangalunga*	?	Indonesia	Celebes	?
Common Palm Civet	*Paradoxurus hermaphroditus*	?	Indonesia	Moluccas	?
Sika Deer	*Cervus nippon hortulorum (mantchuricus)*	1880s	Manchuria	Europe	. . .
Sika Deer	*Cervus nippon nippon*	1880s	Japan	Europe	. . .
Sika Deer	*Cervus nippon taiouanus*	1942	?	Japan	. . .
Fallow Deer	*Dama dama*	Middle Ages	Asia Minor	Central Europe	Parks
Rusa Deer	*Cervus timorensis moluccensis*	1855 1913, 1920	Ceram Moluccas	Aru Islands New Guinea	Hunting Hunting
Rusa Deer	*Cervus timorensis russa*	1680	Java	Borneo	Hunting
Hog Deer	*Axis porcinus*	18th Century	India	Ceylon, Denmark	Hunting
Mouflon	*Ovis musimon*	1869	Sardinia or Corsica	Slovakia	Hunting

Common Name	Scientific Name	Year(s) of Liberation	Country or Place of		Reason for Introduction
			Origin	Introduction	
Indian Buffalo	*Bubalus bubalis*	Recent	India	Andaman Islands	Hunting
3. *Transplanted on the continent*					
Golden Hamster	*Mesocricetus auratus*	?	Syria	Germany	?
European Rabbit	*Oryctolagus cuniculus*	Middle Ages	Europe	Central Europe	?
European Hare	*Lepus europaeus*	?	C. Europe	Sweden, Far East	Hunting
Raccoon-Dog	*Nyctereutes procyonoides*	Recent	E. Asia	Soviet Union	Fur
Sable	*Martes zibellina*	Recent	Trans. to several places		Fur
Stone Marten	*Martes foina*	Recent	Trans. to several places		Fur
Ferret	*Mustela putorius eversmanni*	Recent	Trans. to several places		Fur
Sea Otter	*Enhydra lutris*	Recent	Trans. to several places		Fur
European Mink	*Mustela lutreola*	Recent	Siberia	Far East	Fur
Arctic Fox	*Alopex lagopus*	Recent	Siberia	Kola Peninsula	Fur
B: *Failed to survive:*					
Hog Deer	*Axis porcinus*	1700s	India	Ceylon	Hunting
		1880	India	Denmark	Hunting
Nubian Ibex	*Capra ibex nubiana*	1910s	Asia Minor	Czechoslovakia	Hunting
Goat	*Capra hircus*	1910s	India	Czechoslovakia	Hunting
Chinese Water-Deer	*Hydropotes inermis*	1850	China	British Isles	Parks
Black-tailed Deer	*Odocoileus hemionus columbianus*	1850	N. America	British Isles	Parks
Axis Deer	*Axis axis*	1846	India	Java, Nicobar Is.	Hunting
Indian Muntjac	*Muntiacus muntjak*	1850	India	British Isles	Parks
Reeves's Muntjac	*Muntiacus reevesi*	1850	China	British Isles	Parks
C: *Transplantations of subspecies to range of other subspecies:*					
Roe Deer	*Capreolus capreolus pygargus*	Before 1914	Siberia	Czechoslovakia	Hunting
Maral Deer	*Cervus elaphus asiaticus*	19th Century	Siberia	Eur. Russia	Hunting
American Wapiti	*Cervus canadensis*	19th Century	N. America	Austria	Hunting
Red Squirrel	*Sciurus vulgaris exalbidus*	Recent	Siberia	C. Russia	Fur
European Beaver	*Castor fiber*	1927	Norway	Latvia	Fur
		1935	Norway	Letland, Finland	Fur
Red Deer	*Cervus elaphus*	?	Germany	Norway	Fur
English Red Fox	*Vulpes vulpes*	Recent	British Isles	Sweden	Fur
Siberian Sable	*Martes zibellina*	Recent	Several parts of Soviet Union		Fur
D: *Status unknown:*					
Alpine Marmot	*Marmota baibacina*	Recent	Soviet Union		Fur
Himalayan Marmot	*Marmota bobak*	Recent	Soviet Union		Fur
Large-toothed Souslik	*Citellus fulvus*	Recent	Soviet Union		Fur
Raccoon	*Procyon lotor*	Recent	N. America	Soviet Union	Fur
Corsac Fox	*Vulpes corsac*	Recent	?	Soviet Union	Fur
Arctic Fox	*Alopex lagopus groenlandicus*	Recent	Greenland	Soviet Union	Fur
Russian Desman	*Desmana moschata*	?	?	?	?
Striped Skunk	*Mephitis mephitis*	Recent	N. America	Soviet Union	Fur

The American Gray Squirrel *(Sciurus carolinensis)* has become a serious liability since its introduction into the British Isles. Although several early introductions failed, others resulted in restricted local establishments. The present population probably dates from introductions since 1890, although there are several records of the species before that date. Specimens were liberated in southern and central England, in Scotland and in one locality in Ireland. By 1930, Gray Squirrels occupied approximately 13,350 square miles in the greater part of southeastern England, the Midlands and Yorkshire (Middleton, 1930).

Little is known of the present distribution of the Gray Squirrel in Ireland, where it was introduced before 1938. It is, however, extending its range, and is also spreading in Scotland (Shorten, 1953).

The spread of the Gray Squirrel in England is well documented by Shorten (1946, 1953) who devised a system of grids 10 km. square and related the distribution and spread of the squirrel to them. She also tried to correlate the disappearance of the native Red Squirrel *(Sciurus vulgaris leucourus)* with the spread of the Gray Squirrel. While the American intruder was present in 274 grids in 1937, it occurred in 708 in 1944 and 1945, and had spread into an additional 199 by 1952. Apparently in some areas the spread may be halted by such natural barriers as large rivers with few bridges, or by mountainous or treeless country. In no place does the Gray Squirrel inhabit dense coniferous woods, which are the preferred habitats of the Red Squirrel (Middleton, 1930).

After a period of years, the presence of Gray Squirrels may cause the disappearance of Red Squirrels. In 1952, Red Squirrels seemed to have disappeared from areas in eight counties where Gray Squirrels had become established since 1945 (Shorten, 1953). There is little evidence available regarding competition or antagonism between the two species. Possibly the Gray Squirrel carries a disease which is fatal to the Red Squirrel but not to itself. The occurrence of many epidemics after the first appearance of Gray Squirrels supports this contention (Middleton, 1930).

This American immigrant is a serious pest in Great Britain, where only the Norway Rat is considered worse. It does much damage to many kinds of trees, fruits and plants.

The Nutria *(Myocastor coypus)*, a native of South America, has been introduced on many fur farms in Europe since 1926. In many cases the animals were released when they were considered a liability, and sometimes they escaped. Wild populations are now present in Russia, England, Holland, Denmark, Germany, France and Japan.

In Russia, Nutrias have been imported into Transcaucasia, the Kuban delta, the downstream parts of the Kura and Terek Rivers and the southern part of the Amu-Darja Basin, where they have multiplied. Since 1949, increasing numbers of Nutria pelts have been offered on the market (Schmidt, 1954). Efforts to introduce this fur-bearer into central Russia have failed because of unsuitable climatic conditions. However, the Nutria is successfully established in Armenia, Georgia and the steppes of Shirwan (Lindemann, 1956). Because of low fur prices in 1949, Nutrias were released from several fur farms in Holland. Although the animals are well established, they are readily controlled because of their large size, diurnal habits and trusting ways. According to P. V. Jensen *(in litt.)* several escaped animals are now living in the wild in Denmark, where they are reproducing. In France, Nutrias have escaped from parks in several parts of the country, mostly in the central section. They appear to be maintaining their numbers in the wild state. These rodents were imported from Europe to fur farms in Japan in 1931. A few escaped and established a small breeding population; in 1949 about 500 were known to be present south of Okayama City. Nutrias trample down and eat the rice in the paddy fields (Kuroda, *in litt.)*.

Apart from the more spectacular introductions already mentioned, several other rodents have been imported or transplanted. The Red Squirrel *(Sciurus vulgaris exalbidus)* was introduced into central Russia from several parts of Siberia with the result that thousands are now being harvested (Schmidt, 1954).

European Beavers *(Castor fiber)* were reintroduced from Norway into their former range in Sweden in the 1920s. Specimens also were imported from Norway into Latvia in 1927, and again into Latvia as well as Finland in 1935 (Harper, 1945). Beavers also were transplanted to several parts of the Soviet Union, such as the Kola Peninsula, western Siberia and the Volga delta. The American Beaver *(Castor canadensis)* has also been imported into Russia (Naumoff, 1950).

The Syrian Golden Hamster *(Mesocricetus auratus)* has become established locally in the wild in parts of Germany. Here there exists the possibility that it may become a pest in crop lands and food storage places.

The Fat Dormouse *(Glis glis)* was introduced into the British Isles from continental Europe. Rothschild released a few pairs near Tring in 1886, and there were several subsequent importations. After a slow establishment, the spe-

cies gradually spread into several adjoining counties. It seems to be doing little serious damage, and keeps largely to the neighborhood of houses (Cansdale, 1953).

The Formosan Golden-backed Squirrel *(Callosciurus caniceps thaiwanensis)* was introduced in zoological gardens on the Island of Oshima, south of Tokyo, some time after 1940. It escaped, and in 1950 an estimated population of 20,000 inhabited many parts of the island. These squirrels chase White-eyes *(Zosterops palpebrosa)* from the flowers of the camellia, resulting in lack of fertilization of this plant. Other trees and shrubs are stripped of their bark, and nuts also are eaten. These activities result in a considerable decrease in the production of camellia oil, the island's principal commodity.

The northern Red-backed Vole *(Clethrionomys rutilus)* was introduced in 1870 from Kamchatka to Bering Island, one of the Commander group. Within ten years it spread over all the island from the beaches to the interior mountains. It occurs both in the swamps and on the sand dunes, and has become a pest in the huts of the natives (Palmer, 1899).

Marmota baibacina, Marmota bobak and *Citellus fulvus* have also been transplanted within the Soviet Union (Naumoff, 1950).

The European Rabbit *(Oryctolagus c. cuniculus)* undoubtedly has a much wider distribution in central and western Europe now than in Roman times, and it still seems to be extending its range, assisted by man. It was introduced in the Middle Ages into Germany and Holland for hunting purposes and reached the British Isles from central Europe in the Twelfth Century (Cansdale, 1953). In Denmark it has been released in several places in the past fifty years, but has not increased greatly. About 1920 it crossed the Danish border from an isolated German population released about 1900 (Jensen, *in litt.*). The rabbit has also been released in the Soviet Union (Naumoff, 1950) and in China (Allen, 1938). Rabbits were liberated on one of the islands of the Madeira group in the Fifteenth Century; they increased so rapidly as to seriously deplete the vegetation.

Although rabbits are popular game animals and provide much meat and many skins, they are nevertheless destructive pests in that they raid gardens, kill many tree seedlings and reduce the carrying capacity of pastures for livestock. They also compete seriously for food with the European Hare. The recent myxomatosis outbreak in western Europe has changed the picture completely; rabbits have become very scarce.

Other introduced lagomorphs include the European Hare (*Lepus e. europaeus*) in the Far East (Lindemann, 1956) and also in Sweden, where it is gradually replacing the Alpine Hare *(Lepus timidus)*, possibly because of a higher reproductive potential. A pair of Alpine Hares was introduced from Norway to the Faroe Islands in 1854-55; their descendants have given rise to a new subspecies, *seclusus*. Immediately following their introduction, all the hares turned white in winter, but today they retain their dark coats throughout the year (Bourlière, 1954). This species has also been transplanted from the Scottish Highlands to the southern uplands and to the island areas of the Highlands (Darling, 1947). The Black-naped Hare *(Lepus nigricollis)*, a native of India and Ceylon, has been introduced around Djakarta, Indonesia, and now occurs also near Bogor and Bandoeng (van Bemmel, *in litt.*).

The few transplantations of monkeys in Asia include the Celebes Crested Macaque *(Cynopithecus niger)* to the island of Ambon and the Crab-eating Macaque *(Macaca irus)* to Celebes and the Lesser Sunda Islands from the more westerly islands in the Indonesian Archipelago. The Formosan Rhesus Monkey *(Macaca cyclopis)* escaped from captivity on Oshima Island, south of Tokyo, and multiplied rapidly in the absence of natural enemies; there is some doubt as to whether it occurs in the wild at Kivozumi (Prefecture Chiba), Hindo. The Pig-tailed Macaque *(Macaca nemestrina leonina)* was introduced from India to the Andaman Islands (S. L. Hora, *in litt.*).

The Javan Mongoose *(Herpestes javanicus)* has been introduced to Ambon from other islands in the Indonesian Archipelago. One Palm Civet *(Paradoxurus hermaphroditus)* was introduced throughout the Moluccas and the Lesser Sunda Islands, and the Malay Civet *(Viverra tangalunga)* was imported into Celebes. The Masked Palm Civet (*Paguma* sp.) was imported into Japan in ancient times and again more recently as a cage animal; it probably came from Formosa *(P. taivana)* or from South China *(P. larvata)*. Some evidently escaped, according to sporadic records from Central Hondo and Shikoku. The animal is said to have been caught in the Prefecture of Yamanashi in early times, and again more recently.

The Mouflon *(Ovis musimon)*, although reduced in numbers in its native Sardinia and Corsica, appears to have thrived in various continental areas. It has become established in Germany, Czechoslovakia, Austria, Rumania, European Russia, Holland and Denmark. In 1869, ten were transferred to the Tribec Mountains of Slovakia, where they became established. Several herds are now dispersed over Germany and

Austria. The herd in Holland, numbering about one hundred head, was started in 1918-19. In 1951-52 Mouflons were released on private lands in Southfyn, Denmark (Jensen, *in litt.*). The species was introduced into Italy during the mid-1800s, but has long since disappeared (Harper, 1945). According to Turcek (*in litt.*) Mouflons were introduced to the Crimea and South Ukraine before World War I. It is of interest that a new race developed in the Slovakia range; about 1910 a distinctly different type of sheep was common, in which the rams are darker in color, lack the saddle patch and possess short, thick horns with converging tips (Allen, 1954).

In 1910 two goats, the Bezoar Goat *(Capra hircus)* and the Nubian Ibex *(Capra ibex nubiana)* were introduced from Asia Minor into the High Tatra Mountains of Czechoslovakia. They interbred with the native Ibex *(Capra i. ibex)*, reintroduced since 1901. The hybrids did not do well, possibly because they were born during the dead of winter rather than in spring, as are the native Ibex (Turcek, 1951).

The Indian Buffalo *(Bubalus bubalis)* has been recently introduced into the Andaman Islands from India. The availability of considerable food and the absence of predators have aided its establishment, and it is slowly extending its range (Hora, *in litt.*).

In 1929, seventeen Muskoxen *(Ovibos moschatus)* were introduced from East Greenland to Spitzbergen. This herd appeared to be thriving in 1950 (Anon., 1952a).

Several species of deer have been introduced or transplanted in Eurasia. The Fallow Deer *(Dama d. dama)*, originally from Asia Minor, has been widely imported in captivity, and also liberated in the wild. In Denmark it was mentioned in the literature as early as 1231, having been introduced by the Danish Kings for hunting; it now occurs in deer parks as well as in the wild, and its numbers were estimated at 3,300 head in 1950 (Jensen, *in litt.*). Fallow Deer have been in Germany since the Middle Ages, but their population is small. They were introduced into the Bialowies Forest of western Russia about 1890, but required special care; none have been observed since 1930 (Lindemann, 1956).

Sika Deer have been introduced at several places in western Europe as well as in eastern Asia. Two subspecies reached the British Isles, *Cervus n. nippon* from Japan and *C. n. mantchuricus (= hortulorum)* from Manchuria, near Loch Rosque from 1880 to 1890. Their range still centers about the Achnasheen area. Another introduction in 1893 still survives at Carradale, Kintyre (Darling, 1947). Sika Deer are numerous in parts of the Midlands and in the southern counties from Kent to Dorset (Matthews, 1952). H. G. Lumsden (*in litt.*) reports them present near Inniskillen, Ireland. The Japanese race first reached Denmark around 1900, and was later liberated from captivity; about 500 of these animals are now living in the wild (Jensen, *in litt.*). Sika Deer are still reported in the wild in France. In Japan, *Cervus nippon taiouanus* was released on Oshima Island, south of Tokyo, about 1942-43; fifty were observed here in 1950 (Kuroda, 1955). The Manchurian Sika *(C. n. hortulorum)* has been released in the Soviet Union (Naumoff, 1950).

The Hog Deer *(Axis porcinus)* was introduced to the western parts of Ceylon during the Dutch occupation in the Eighteenth Century. Here it multiplied and persisted until about 1920, but since then, with increased human population and heavier hunting pressure, it has been practically extirpated (C. W. Nicholas, *in litt.*). This species, from India, was liberated on Samsö Island, Denmark, in 1880, but no longer exists there (Jensen, *in litt.*).

The Axis Deer (*Axis axis*), introduced from India to the Nicobar Islands in 1846, seems to have disappeared there, for reasons unknown (Hora, *in litt.*).

Reeves's Muntjac *(Muntiacus reevesi)* and the Indian Muntjac *(Muntiacus muntjak)*, as well as the Chinese Water Deer *(Hydropotes inermis)* and the Black-tailed Deer *(Odocoileus hemionus columbianus)*, have apparently escaped or been released from parks in the British Isles since 1850 (Matthews, 1952). They seem to survive in the wild in small numbers. Barking Deer have been reported introduced from Bali to Lombok (Everett, *in litt.*). Sambar Deer (*Cervus unicolor*) have been transplanted from the Philippine Islands to Guam and Rota (Baker, 1946).

White-tailed Deer *(Odocoileus virginianus)* from Minnesota have twice been released in Finland. One buck and four does, liberated 100 miles north of Helsinki in 1934, had multiplied to more than 200 by 1947. A further introduction of three bucks and three does was made in 1948 (Connelly, 1948). The next year some damage to forests and isolated farms was noted (Salmi, 1949).

Deer have been widely transported throughout the eastern part of the Indonesian Archipelago; in some instances the circumstances are known. Rusa Deer *(Cervus timorensis russa)* were introduced into Ambon from Java and later from Celebes (where they were not native) during the Seventeenth Century. In the Aru Islands, deer *(Cervus timorensis moluccensis)* were imported from Ceram in 1855, and are now numbered in the thousands. In South Borneo Rusa Deer were

introduced near Mataram about 1680; these increased to enormous herds in the Nineteenth Century, but have since declined (van Bemmel, 1952). In Netherlands New Guinea, *C. t. moluccensis* now occurs on the Onin Peninsula (introduced from Ceram in 1913) as well as on the eastern coast of the "Birdshead" (around Manokwari) and near Hollandia, the latter stock from Halmaheira in 1920 (Westermann, 1947).

Three species of deer have been transplanted in Europe with poor results. The Siberian race of the Roe Deer *(Capreolus capreolus pygargus)*, released in Czechoslovakia prior to World War I, hybridized in some localities with the smaller native race; crosses involving a native female produced a fetus too large for parturition. Effects of crosses with native males are still perceptible in bucks with abnormally high and thick antlers (Turcek, 1951). In the British Isles, Siberian Roebuck have escaped from parks since 1850 (Matthews, 1952); they have also been transplanted within the Soviet Union (Naumoff, 1950).

The transplantation of German Red Deer *(Cervus elaphus)* into Norway has apparently resulted in the virtual extermination of the species there, probably because the German strain was less hardy. A few hundred American Elk *(Cervus canadensis)* were introduced to Austria by Francis Joseph I (Lorenz, 1953). Asiatic elk have also been transplanted in Russia (Naumoff, 1950).

Central Maral Deer *(Cervus elaphus asiaticus)* from Asia and American elk *(Cervus canadensis)* were introduced into European Russia in the days of the Czars. Hybridization between the two species resulted in the development of animals with antlers having less spread, fewer points and poorly developed burrs (Lindemann, 1956).

Other ungulates transplanted within the Russian orbit include the European Bison *(Bison bonasus)*, the Siberian Ibex *(Capra ibex sibirica)* and the Wild Boar *(Sus scrofa)* (Naumoff, 1950).

Many carnivorous fur-bearers have recently been transplanted in the wild, especially in the Soviet Union. The Raccoon-dog *(Nyctereutes procyonoides)* from extreme eastern Asia was introduced into the Baltic Republics and into White and Middle Russia from Smolensk to the Urals. In central Russia this animal is now one of the principal fur producers, but in Siberia its fur proved to be less valuable and the animals soon competed seriously with the more highly regarded native mustelids (Lindemann, 1956). It is reported that in the Caucasus the Raccoon-dog changed its food habits from fish and crabs to game birds, hares and poultry.

Several forms of Mink have been transplanted for their furs. *Mustela vison* from North America has escaped from fur farms in Norway, Sweden, Denmark, the Soviet Union and Iceland. Their status in Norway is described by Wildhagen (1956). In the Scandinavian countries they are a serious problem because of their depredations; whether they are yet fully established in Denmark is not certain (Jensen, *in litt.)*. The Iceland escape is rather recent, but damage to native wildlife already has been reported (Anon., 1953b).

The Siberian Weasel *(Mustela sibirica coreana)* was imported from South Korea to Japan after 1930, where it escaped from fur farms and bred with the native *M. s. itatsi* which it is gradually replacing; it has already extended into southwestern Hondo and the eastern parts of Shikoku. The Japanese race, introduced into Hokkaido before 1901, has increased and spread; it was further transplanted to two small islands off Hokkaido in 1933, and in 1948 was imported into Okujirijima in the hope of exterminating *Rattus norvegicus* and *Apodemus*.

Lindemann (1956) refers to the introduction of the European Mink *(Mustela lutreola)* into the Far East.

An interesting case of differential survival is recounted by van Koersveld *(in litt.)*. In 1931 nine Ermines *(Mustela erminea)* and 102 weasels *(Mustela n. nivalis)* were introduced on the island of Terschelling, Holland, to diminish an abundance of rabbits and rats. By 1953, the Ermines had increased to a high population, but the weasels had entirely disappeared. A bounty is now set on the Ermines, which kill many wild birds and poultry.

Sables have been transplanted from the Trans-Baikal to several parts of the Ural and Altai Mountains. The Kamchatkan Sable *(Martes zibellina kamtshadalica)* was introduced into western Siberia, where it has interbred with the native form. The resultant hybrids have heavier and more valuable furs than the native animal (Lindemann, 1956).

Other mustelids introduced or transplanted in the Soviet Union include the Stone Marten *(Martes foina)*, the Skunk (probably *Mephitis mephitis)*, the Siberian Weasel *(Mustela sibirica)*, the Sea Otter *(Enhydra lutris)* and the Ferret *(Mustela putorius eversmanni)* (Naumoff, 1950).

The North Siberian Polar Fox *(Alopex lagopus)* has been released on the Kola Peninsula (Lindemann, 1956). The introduction of Red Foxes *(Vulpes vulpes)* from England to Sweden may be responsible for the appearance of numerous "Samson foxes"—individuals lacking guard hairs and therefore of little value for their fur. Alaskan Silver Foxes *(Vulpes fulva alascensis)* were released in Finland in 1938 with the idea of producing a good cross-fox hybrid between it

and the native Red Fox, and interbreeding seems to be occurring. In European Russia large numbers of North American Silver Foxes were released (Schmidt, 1954). Naumoff (1950) lists also *Vulpes fulva, Vulpes corsac* and *Alopex lagopus groenlandicus* as introductions in the Soviet sphere.

The Raccoon *(Procyon lotor)* is the only other carnivorous fur-bearer introduced into the Soviet area which is mentioned by Naumoff (1950). It is present in the Far East (Ussouri) and in European Russia.

North America:

North America, and the United States in particular, seems to have received an unduly large number of introductions. Why this continent, with a rich and varied native mammalian fauna, should have been subjected to the importation of numerous exotics is not clear, but a possible explanation is the dependence of the colonists upon hunting and trapping for food and clothing. The spread of settlements from Atlantic to Pacific led to the virtual annihilation of some important and valuable animals, such as the Beaver, the Bison and other ungulates. The depletion of several major game species did not necessarily result in the loss of hunting as a privilege, but led to the use of other, perhaps less desirable, species as game. North Americans have come to consider hunting and trapping as a portion of their heritage, and many of the introductions and transplantations of mammals may be related directly to attempts to provide added materials to bolster the reduced numbers of native mammals.

In no case have foreign implants been an unqualified success; generally they have been failures. Several colonies of exotic monkeys, of various species, are established in the Caribbean region (Miller & Kellogg, 1955). The last few years have seen the successful introduction of the Barbary Sheep *(Ammotragus lervia)* into New Mexico (O'Conner, 1953), the release of the European Rabbit *(Oryctolagus cuniculus)* in Pennsylvania and the liberation of the Chinchilla *(Chinchilla* sp.) in California (Voris *et al.*, 1955).

Accidental introductions or escapes take place from time to time, but seldom are these followed by the permanent establishment of the species. Examples of failures are the Blue Fox *(Alopex lagopus)* in Minnesota (Bailey, 1929) and the Coatimundi *(Nasua narica)* in Oklahoma (Glass & Hanson, 1952) and in Indiana (Lyon, 1923).

Worthy of special studies in themselves are the details of the many transplantations, from state to state, of Pronghorns *(Antilocapra americana)* (Fisher, 1942; Nichol, 1942), American Elk *(Cervus canadensis)* (Atwood, 1938; Kirk, 1923; Scheffer, 1941), Muskrat *(Ondatra zibethicus)* (Dickey, 1923; Eyerdam, 1932; Storer, 1937) and other favored game and fur-bearing mammals (Dice, 1927; Dixon, 1929; Bailey, 1936). These species have been transplanted widely and, as a result, several local races, particularly of the Elk and Muskrat, have been mixed.

Countless experimental plantings have been tried and a few examples may be cited. On Anticosti Island, in the Gulf of St. Lawrence, have been made introductions of Moose *(Alces alces)*, American Elk, Whitetail Deer *(Odocoileus virginianus)*, Bison *(Bison bison)*, Mink *(Mustela vison)*, Fisher *(Martes pennanti)*, Red Fox *(Vulpes fulva)*, Beaver *(Castor canadensis)*, Muskrat and Varying Hare *(Lepus americanus)* (Newsom, 1937). On Lanz Island, British Columbia, Mink were imported from Vancouver Island about 1938; by 1950 they were so plentiful as to force out the pelagic birds which formerly nested there. From here, these Mink populated Cox Island, on which Raccoons *(Procyon lotor)* from Vancouver had also been planted in 1938. The Raccoons became established, but had not by 1950 become as injurious as the Mink (Clifford *et al.*, 1951).

Massachusetts has introduced, on the islands of Nantucket and Martha's Vinyard, Varying Hares, Black-tailed Jackrabbits *(Lepus californicus)*, European Hares *(Lepus europaeus)*, Florida Cottontails *(Sylvilagus floridanus)*, Red Fox, Prairie Dogs *(Cynomys ludovicianus)* and Fallow Deer *(Dama dama)*. The foxes and Prairie Dogs became such pests that they were exterminated; the Fallow Deer seemingly compete for food with the White-tailed Deer on Martha's Vinyard; the Florida Cottontail probably competes with the native *Sylvilagus transitionalis*. It is believed that western rabbits introduced tularemia to these islands (Starrett, *in litt.*).

In New York State, since 1886, released game and fur-bearing mammals have included Raccoon, Red Fox, Coyote *(Canis latrans)*, Timber Wolf *(Canis lupus)* Beaver, Muskrat, Fox Squirrel *(Sciurus niger)*, Varying Hare, Cottontail, European Hare, Pronghorn, Black-tailed Deer *(Odocoileus hemionus)*, White-tailed Deer, Moose, Elk, Red Deer *(Cervus elaphus)*, Japanese and Siberian Deer and Wild Boar *(Sus scrofa)*. Only the Beaver and White-tailed Deer plantings were successful (Bump, 1940). The State of Washington has witnessed the establishment of the Virginia Opossum *(Didelphis marsupialis)*, eastern Fox Squirrel, Gray Squirrel *(Sciurus carolinensis)*, eastern Cottontail, Nutria *(Myocastor coypus)* and the Pronghorn (Buechner, 1953; Dalquest, 1948). In Michigan, Jack-

rabbits *(Lepus townsendii)*, European Hares, Nutria, Reindeer, Moose and Elk have been introduced (Blouch, 1954; Ruhl, 1940). Alaska has seen the introduction of ground squirrels *(Citellus undulatus)*, Raccoons, Blue Foxes, Black-tailed Deer, Reindeer, Roosevelt Elk, Bison and Muskoxen (Murie, 1940; Scheffer, 1947; Palmer, 1954). Muskrats and ground squirrels failed to survive on the Pribilof Islands (Preble, 1923).

In Texas, several ranchers have experimented with exotic game species. At least some of this stock is on open range and hence might possibly become established in the wild. The King Ranch has introduced White-tailed Deer, Elk, Japanese Fallow Deer, Indian Blackbuck *(Antilope cervicapra)* and Nilgai Antelope *(Boselaphus tragocamelus)*; only the last two survived (Lehmann, 1948). The Bar-O Ranch has stocked the Sardinian Mouflon *(Ovis musimon)* which later crossed with domestic sheep, the Blackbuck, Asiatic Serow *(Capricornis sumatraensis)*, and Aoudads. The Rickenbacker ranch has kept European Fallow Deer, Roe Deer *(Capreolus capreolus)*, Asiatic Sambar *(Cervus unicolor)* and Blackbuck on a large scale (O'Conner, 1953). Some zoological gardens in Texas are selling Axis Deer and antelopes for the stocking of ranches. It is estimated that at least 1,000 wild Blackbuck exist in Texas alone today, and they are on the increase (Stilwell, 1955). Similar instances of large scale introductions or transplantations might be related for California (Storer, 1931, 1933), North Carolina (Anon., 1953a), Ohio (Hicks, 1940), Ontario (Soper, 1923), Pennsylvania (Anon., 1944), Saskatchewan (Forsyth, 1942), Utah (Popov & Low, 1953) and elsewhere.

Kangaroo Rats *(Dipodomys ordii)* have been introduced on the sand dunes on the shores of Lake Erie, near Fairport, Ohio, and are established (Bole & Moulthrop, 1942).

Happily, the short-sighted policy of wholesale introduction on a hit or miss basis is no longer as common as it once was. Missouri has recently stopped its long practice of supplying Cottontails to many other states in the northeastern United States. Still, there are reports of plantings of Great Plains Jackrabbits *(Lepus californicus)* in Kentucky (Myers, 1952) and of European Rabbits from the San Juan Islands off the coast of Washington to Pennsylvania and elsewhere (Anon., 1954b).

Table 2 summarizes the status of introduced mammals in North America. The following introductions or transplants are discussed in detail.

The Nutria *(Myocastor coypus)* has been imported for its fur in many places in the United States and Canada. Escapees or releases from fur farms have survived in the wild and several local populations have increased. The animal seems best established in the marshes of the southeastern states (Dozier, 1951) and of Oregon, where it is the subject of much debate. Its pelt commands a low price and is in little demand. In Louisiana it is increasing rapidly and competing seriously for food with the more valuable muskrats, which are reported on the decline (Ashbrook, 1953). It was reported on the Pacific coast by 1942 (Larrison, 1943) and is now in Washington (Dalquest, 1948). In California most of the escaped Nutrias were killed (Storer, *in litt.*). Colonies are reported living in a feral state in Montana (Jellison, 1945), Texas (Petrides, 1950; Swank & Petrides, 1954), Ohio, Kansas and Michigan.

The Muskrat was transplanted to Vancouver Island, to other islands off the coast of British Columbia, and to several localities in California (Storer, 1937). The population has spread since the original releases were made.

From 1888 to 1911 European Hares were liberated at various places, and some of these releases survived (Osborn, 1933). The earliest well-authenticated releases were in Brant County, Ontario, in 1912 (Dymond, 1922). From here they spread rapidly, and by 1923 were reported in several localities in Wellington and Waterloo Counties (Soper, 1923). They were further introduced near Thunder Bay, Ontario (Allin, 1950). They are now reported in all of southern Ontario (Reynolds, 1952). These hares, although good game animals, are often pests, consuming crops and damaging orchards. By 1950, they were considered to be established beyond hope of eradication in southern Ontario and in Michigan (Cahalane, 1950). In addition, they have also invaded northern Wisconsin and Minnesota, and range from the St. Lawrence across northeastern New York (Hamilton, 1952) and extreme western New England into New Jersey and eastern Pennsylvania.

The introduction of the European Rabbit on the mainland of North America is recent and may still be susceptible of control. On other continents this burrowing rabbit seriously competes for forage even with sheep, undermines buildings, kills vegetation and causes erosion. A population has existed on the San Juan Islands off the coast of Washington, perhaps since the days of the Hudson's Bay Company occupation (Thompson, 1955). In 1900 and thereafter more "Belgian Hares" or "tame rabbits," a domestic form raised for fur and meat, were released by the lighthouse keeper on Smith Island to supplement the earlier population. Introductions followed on several other islands of the San Juan group. Numbers increased and reached plague

TABLE 2: MAMMALS INTRODUCED OR TRANSPLANTED IN NORTH AMERICA

Common Name	Scientific Name	Year(s) of Liberation	Country or Place of Origin	Country or Place of Introduction	Reason for Introduction
A: *Established: increased in numbers and/or range:*					
Raccoon	*Procyon lotor*	1932	Florida	Bahamas	Curiosity
Mink	*Mustela vison*	1938	Vancouver	Scott Islands, B.C.	Fur
European Red Fox	*Vulpes vulpes*	18th Century	W. Europe	N.E. U.S.A.	Hunting
Nutria	*Myocastor coypus*	1940?	S. America	Louisiana	Fur
European Hare	*Lepus europaeus*	1912	Europe	Ontario	Sport, food, fur
European Rabbit	*Oryctolagus cuniculus*	1900 1953	Europe	Washington Pennsylvania	Fur, food Hunting
Wild Boar	*Sus scrofa*	1912	Germany	N. Carolina	Sport
Fallow Deer	*Dama dama*	1938	?	Nebraska	Sport
Peccary	*Pecari angulatus*	?	Yucatan	Cozumel Island, Mexico	Food?
Kangaroo Rat	*Dipodomys ordii*	?	S.W. U.S.A.	Ohio	Curiosity
Jaguarundi	*Felis yagouaroundi*	Before 1942	Central or S. America	Florida	?
B: *Survived but did not spread:*					
Three-toed Sloth	*Bradypus griseus*	1925	Panama	Barro Colorado Island	Curiosity
Sambar Deer	*Cervus unicolor*	1900	Asia	Florida	Sport
Fallow Deer	*Dama dama*	?	Europe	Texas	Sport
Roe Deer	*Capreolus capreolus*	?	?	Texas	Sport
Blackbuck	*Antilope cervicapra*	?	India	Texas	Sport
Nilghai	*Boselaphus tragocamelus*	?	India	Texas	Sport
Mouflon	*Ovis musimon*	?	Sardinia	Texas	Sport
Serow	*Capricornis sumatrensis*	?	Asia	Texas	Sport
Aoudad	*Ammotragus lervia*	1950	Africa	New Mexico	Sport
Axis Deer	*Axis axis*	1930s	India	Florida	Escapees
C: *Failed to survive:*					
Coatimundi	*Nasua narica*	1950	?	Oklahoma	Escaped
Blue Fox	*Alopex lagopus*	1927	Arctic	Minnesota	Escaped
Ground Squirrel	*Citellus undulatus*	1899	Alaska	Pribilof Is.	Food for foxes
Muskrat	*Ondatra zibethicus*	1913	Nushagak	Pribilof Is.	Fur
Red Deer	*Cervus elaphus*	?	?	?	Sport
Sika Deer	*Cervus nippon*	?	Japan	?	Sport
German Deer	*Cervus elaphus*	?	Germany	?	Sport
Fallow Deer	*Dama dama*	?	Japan	Texas	Sport
Roe Deer	*Capreolus capreolus*	?	Siberia	?	Sport
D: *Successful transplantations* (only a partial list, covering little-known cases):					
Marten	*Martes americana*	1953 1954	Ontario Montana	New Hampshire Wisconsin	Aesthetic Aesthetic
Muskox	*Ovibos moschatus*	1930	Greenland	Alaska	Food, clothing
Armadillo	*Dasypus novemcinctus*	1918	Mexico	Florida	Curiosity
Mountain Goat	*Oreamnos americanus*	1948	Rocky Mts.	S. Dak., Colo.	Hunting

proportions by 1924, when the rabbits were estimated at over thirty to the acre on Smith Island. Wholesale poisoning was undertaken, and nearly 2,000 were probably killed (Couch, 1929). But the rabbits have persisted, and of late are being introduced elsewhere. Feral stocks also occur on South Farallon Island, 30 miles west of San Francisco (Storer, *in litt.*). Shipments have recently reached Ohio, Pennsylvania, Indiana and Wisconsin (Barnes, 1955). The implicit dangers have been publicized (Anon., 1954b; Thompson, 1955). Perhaps, as was the case in Australia and New Zealand, these initial releases may prove unsuccessful, and this new exotic may not further extend its range into North America.

The Nine-banded Armadillo (*Dasypus novemcinctus*), which gradually has been extending its range northward into Texas since the 1880s, was probably introduced into Florida during World War I (Bailey, 1924). It thrived, and by 1952 occurred over all the state except the swampy southwestern portion and possibly the western panhandle (Neill, 1952). It is regarded as highly undesirable because its burrowing activities undermine buildings, damage gardens and penetrate dikes and levees; on the other side of the picture, the armadillo's burrows provide homes for other animals, its meat is edible, and its horny armor is made into novelties for the tourist trade. It now also occurs in Arkansas, Louisiana, New Mexico and Oklahoma, and has been reported from Alabama, Georgia, Kansas and Missouri (Fitch *et al.*, 1952). In part, this spread appears to be by natural means; its course has been well summarized by Buchanan (1955).

Introduction of Wild Boars *(Sus scrofa)* from the Harz Mountains of northern Germany, primarily for sport, began in 1912 with the arrival of fifteen males and fifteen females. They were kept in a 600-acre enclosure near Hooper Bald, North Carolina, until 1920, when about 100 escaped and persisted in the wild (Stegeman, 1938). They were decimated by hog cholera in 1932, but by 1937 it was estimated that there were about 230 in the region. Some of these were released near Carmel, California, in 1924 and persisted at least until 1938 (Shaw, 1940). Wild Boars readily breed with domestic swine. They are regarded by some as desirable game animals, but also they are harmful to vegetation and to ground-dwelling animals. Their greatest population is currently in the mountain forests of eastern Tennessee, but they exist also in Georgia, North Carolina, Oregon, Texas and on the Corbin Preserve in New Hampshire (Baynes, 1923; Cahalane, 1950; Scheffer, 1941).

The introduction of the Moose into Newfoundland (Pimlott, 1953) may be cited as an instance of the establishment of a mammal which greatly augmented the big game resources of the province and which apparently filled a niche at least partly vacant. Two introductions were made, in 1878 and in 1904. The second attempt resulted in complete establishment. In twenty years the radius of distribution had extended to at least 80 miles from the point of release. At present the species is well established on the entire island, with a bull kill of approximately 14,000 over a period of eight years. Moose have also been introduced into Labrador.

As recently as about 1938, some sixty white Fallow Deer (*Dama dama*), original source unknown, were released on the Hall Ranch ten miles northwest of Petersburg, Boone County, Nebraska. They have reproduced and spread, being reported in 1955 from five counties in central Nebraska (Packard, 1955), where they do some damage to orchards and to crops.

Sambar Deer (*Cervus unicolor*) from a zoological park were released on St. Vincent's Island, near Appalachicola, Florida, in 1900. They have since reproduced and thrived.

The Greenland Muskox (*Ovibos moschatus*), indigenous to the northern mainland and to many parts of the Arctic islands, has been introduced on Nunivak Island, Alaska, where it competes directly with the introduced Reindeer.

Aoudads or Barbary Sheep (*Ammotragus lervia*) have recently been introduced into New Mexico (O'Connor, 1953) and have been promoted for release as game animals in Texas. A large herd is established in the wild on the St. Simeon Ranch near San Luis Obispo, California (Lindemann, *in verbis*).

Dwindling herds of Bighorn Sheep (*Ovis canadensis*) in our western mountains have been supplemented by stock from British Columbia. Twenty individuals were released in the Hart Mountains of eastern Oregon in 1954, and others in several localities in Colorado, Montana and New Mexico (Buechner, 1956).

There is some evidence that the present Red Fox of the eastern United States is a direct descendant of the European Red Fox (*Vulpes vulpes*) which was introduced between 1650 and 1750 from England for fox hunting (Gilmore, 1946).

On Barro Colorado Island, in the Panama Canal Zone, six Three-toed Sloths (*Bradypus griseus*) from nearby Frijoles were released in 1925 (Enders, 1930). Their present status is not known.

In 1942, Jaguarundis (*Felis yagouaroundi*) were reported in Florida. These animals are believed to have been released deliberately at Chiefland and Hillsborough River State Park. Repeated observations of animals believed to be Jaguar-

undis suggest that they are present in the following areas: Dunellon through Chiefland to Jena, eastern Marion County; the south end of the central Florida ridge in Osceola, Polk and Highlands Counties; Everglades National Park; and possibly Hillsborough County. Specimens identified as Jaguarundis have been obtained from Jena and near Lake Placid. The animals seem to prefer areas of thick brush near water. Most of the sight-records were made while they were raiding chicken coops and poultry yards (Neill, *in litt.*).

Axis Deer (*Axis axis*) escaped in Volusia County, Florida, in the 1930s, and they are now known from four counties east of the St. John's River. Since 1951, they have been protected by state law (Allen & Neill, 1954).

The Mountain Goat (*Oreamnos americanus*) was transplanted from its original range in the Rocky Mountain area to the Black Hills in South Dakota, where the species is thriving. It was also introduced into Colorado, at least three of the eleven animals released in 1948 still surviving in 1954 (Yeager, *in litt.*), and into several areas in central Montana (Cahalane, *in litt.*).

Pine Martens (*Martes americana*) have been transplanted during recent years to states where they had been exterminated. Reintroduction from Ontario into New Hampshire appears to be successful (Monahan, 1953). Martens also were transplanted from Montana to Wisconsin.

Bison have been introduced (reintroduced?) and established in northern Sonora, Mexico. Whitetail Deer, reintroduced in the mountains of central Mexico, have failed to survive because of heavy hunting pressure to which they are subjected (Villa-R., *in verbis*). Elk have also been introduced or reintroduced in Waluula.

Peccaries (*Pecari angulatus*) on Cozumel Island, Quintana Roo, Mexico, have been described as a subspecies (*nana*), but it is believed that these animals were introduced from the mainland and that the subspecific characters (small size) are the result of heavy hunting pressure which allows few animals to attain more than two years of age (Hershkovitz, 1953).

South America:

South America, with a continental area larger only than Australia, has been isolated for long periods of geological history. This separation from the other continents, together with major barriers within South America such as the western Cordillera, the tropical forests of the Amazon basin, and the Pampas, has resulted in differentiation of a unique mammalian fauna. Because many native mammals, especially carnivores and ungulates, although specialized, seem to be more primitive than other allied forms living elsewhere, the South American fauna may be highly susceptible to deleterious effects by more highly developed competitors from other continents as well as by intracontinental introductions.

Table 3 summarizes the status of introduced and transplanted mammals in South America.

The European Rabbit (*Oryctolagus cuniculus*) was introduced on islands in the Beagle Channel, Tierra del Fuego, about 1880, by Thomas Bridges, a missionary. These rabbits, brought from the Falkland Islands, were introduced to provide food both for castaways and for the natives, and care was taken to avoid introduction on the mainland. On some islands the rabbits reproduced rapidly, while on others they failed to survive because of predation by birds, hunting pressure by the Indians (who used dogs), or because the land was too rocky or wet for burrowing (Bridges, 1949). Eventually the rabbits reached the mainland and have spread northward, west of the Cordillera, at least as far as Vallenar, Chile. They caused considerable damage to the flora, destroying young pines (*Pinus insignis*) and the native grass cover (Mann, *in litt.*). The European Rabbit is also reported established in Argentina (Sanborn, *in litt.*).

The European Hare (*Lepus europaeus*) was introduced into Argentina in 1880, and has spread to Chile during the present century. It causes much damage to pastures and is found in large numbers in central and southern Chile, north at least to Illapel, and at elevations as high as 2,600 meters (L. E. Peña, *in litt.*). The pelts of the European Hare and European Rabbit are used in various industries, and 50,000 skins were sold in Punta Arenas in 1939. According to C. C. Sanborn (*in litt.*) this hare was introduced into Uruguay and also Tierra del Fuego. He reported range damage by these animals in Patagonia.

The Mongoose (*Herpestes auropunctatus*) was introduced into British Guiana on the mainland of South America from Caribbean stock after 1872. It has multiplied and spread to settled areas, but does not seem to have penetrated farther. The dense tropical forests, the many wide rivers and competition with native predators have been suggested as factors which have limited its spread (Westermann, 1953).

Like other continents, South America has received its share of exotic ungulates. About thirty years ago Red Deer and Fallow Deer were imported for aesthetic and game purposes from a German zoo and liberated on various estates between Temuco and Puerto Montt, Chile; they have reproduced and exist in semi-

confinement (Mann, *in litt.*). On the island of Lago Ranco, Province of Valdivia, wild herds of Red Deer have been reported (Peña, *in litt.*). Red Deer were also introduced between 1916 and 1918 by Pedro Luro in the province of La Pampa, Argentina, and they compete for food with domestic stock. They thrive in the region of the Cordillerana de Neuquen and north of Chubut, and compete strongly with the native Huemul (*Hippocamelus bisulcus*) and Pudu, and are a serious pest to agricultural interests (Crespo, *in litt.*). In Argentina, Fallow Deer have been introduced on various estates in the vicinity of Buenos Aires, but they have not become serious pests (Cabrera & Yepes, 1940; Crespo, *in litt.*). Axis Deer (*Axis axis*) have been introduced in the province of Santa Fé in Argentina (Crespo, *in litt.*) and on farms near Belo Horizonte in Brazil (Maia, *in litt.*); they are in semi-confinement and exist in small numbers. American Elk (*Cervus canadensis*) have been imported to Argentina, according to Murie's (1951) map, but whether these animals were liberated or confined is not known. The report of the introduction of the Bush-Pig (*Potamochoerus*) to South America by the early slave-traders (Simoons, 1953) is viewed with doubt, for the observations are probably confused with descriptions of the native peccaries.

Several mammals have been transferred from one part of the continent to another, occasionally with unfortunate results. The Kinkajou (*Potos flavus*) was introduced (from northern South America?) to the Isle of Juan Fernandez, Chile, "for the purpose of eating the rats which exist there (!), but today is a serious danger for birds . . . destroying them." (Peña, *in litt.*).

Two kinds of Armadillo (*Euphractus sexcinctus* and *Zaedyus pichiy*) have been recorded as introduced as pets from Argentina (as early as 1847) and established in central Chile (Osgood, 1943). Correspondents (Mann, Peña) have failed to confirm the existence of these two animals in the wild state in Chile, and doubt the veracity of the records. Seemingly, if these armadillos are established in Chile, they are neither numerous nor widespread.

The introduction of several pairs of coati (*Nasua* sp.) and of a mustelid (*Vison* sp. [*sic* —the mink?]) about 1940 in the vicinity of Lago Todos Santos, Chile, seems to have been unsuccessful, for these animals have not been seen again (Mann, *in litt.*).

It is gratifying to learn that some South Amer-

TABLE 3: MAMMALS INTRODUCED OR TRANSPLANTED IN SOUTH AMERICA

Common Name	Scientific Name	Year(s) of Liberation	Country or Place of Origin	Country or Place of Introduction	Reason for Introduction
A: *Successful introductions:*					
European Rabbit	*Oryctolagus cuniculus*	1880	Europe via Falkland Is.	Tierra del Fuego	Food
European Hare	*Lepus europaeus*	1880 ?	Europe Europe	Argentina Brazil	Food
Red Deer	*Cervus elaphus*	1920s 1916	Germany	Chile Argentina	Sport and Aesthetic
Fallow Deer	*Dama dama*	1920s	Germany Europe	Chile Argentina	Sport and Aesthetic
Axis Deer	*Axis axis*	?	? India	Brazil Argentina	Sport and Aesthetic
Mongoose	*Herpestes auropunctatus*	After 1872	India via West Indies	British Guiana	Rat control
B: *Successful transplantations:*					
Six-lined Armadillo	*Euphractus sexcinctus*	?	Argentina	Central Chile	?
Pichiy	*Zaedyus pichiy*	1847	Argentina	Central Chile	As pets
Kinkajou	*Potos flavus*	?	Northern S. America	Isle of Juan Fernandez, Chile	Rat control
C: *Unsuccessful transplantations:*					
Coati	*Nasua* sp.	1940	Northern S. Amerca?	Lake Todos Santos, . . . Chile	
Mink?	*Vison* sp. (*sic*)	1940	?	Lake Todos Santos, . . . Chile	

duction of foreign animals: "In the past few ican countries have taken steps to prevent introyears strict government control has been exercised over the introduction of new animals, paying attention to the evident danger which these animals signify for a country of so labile a biotic equilibrium as Chile, whose flora and fauna are, for the most part, of ancient stock and therefore very susceptible to destruction by modern competitors." (Mann, *in litt.*).

Australia:

Australia furnishes one of the best examples of the destructive effect of exotics. Introductions, both of the rabbit and other mammals, have had results disastrous both to the native fauna and to man himself.

Free from the controlling factors of their original habitat, European Rabbits attained incredible numbers. They converted millions of acres of good agricultural country into semidesert by denuding the plant cover and by girdling trees. This resulted not only in a decreased carrying capacity of the range for domestic stock, but also in the rapid disappearance of many specialized marsupials which could not stand the competition. Some marsupials have thus become extinct; others, fortunately, can live in areas too dry for rabbits, and some are arboreal.

Introduced foxes, ferrets, weasels, and feral dogs and cats have wrought havoc among the indigenous fauna. Generally the small marsupials with poorly developed defense mechanisms suffer severely from predation by these placental mammals which are more effective than the native marsupial predators.

Introduced deer have done less harm in Australia than in New Zealand, probably because the Australian habitat is less favorable for them. However, an appraisal of deer damage to forest reproduction and agricultural crops may prove them to be more destructive in Australia than has been supposed.

Table 4 lists the mammals which have been introduced into Australia.

Although further introductions are now rigidly prohibited, legislation regarding exotics already present does not always appear to be reasonable. The contradictory nature of the game laws is shown by the complete protection of deer in Queensland and their partial protection in Tasmania, while there are open seasons on kangaroos in both these states.

Australia's greatest curse, the European Rabbit (*Oryctolagus cuniculus*), was brought to Port Jackson with the first settlers in 1788, and presumably to the other early settlements in Australia and Tasmania. The progenitors of the present hordes are generally believed to be the 24 released for sporting reasons at Barwon Park (near Geelong, Victoria) by Thomas Austin in 1859 (Stead, 1928). It is possible that domestic escapees may have become feral before 1859. Old records indicate many rabbits in Tasmania by 1825. They were also released on various islands at early dates as food for castaways. On many of these islands they did not prosper (Calaby, *in litt.*). There are none today on Kangaroo, King, Flinders or Cape Barren Islands.

Six years after the initial release, Austin had killed 20,000 rabbits on his estate and estimated that at least 10,000 remained. From Victoria, rabbits spread rapidly in all directions, unhampered by any natural controls. By the late 1870s they had crossed the Murray River into New South Wales; they soon populated thousands of square miles here and crossed into Queensland. In vain, thousands of miles of rabbit-proof fences were thrown up; poisoning campaigns killed not only large numbers of rabbits, but also livestock and native species (Stead, 1928). The rabbit has now apparently reached the limits of its range; it seems unable to penetrate the tropical zone, and is very scarce in the arid interior.

The rabbits' damage to vegetation is unbelievable. Vast areas of tree scrub have been cleared by debarking mature trees and eating young seedlings, and in turn unpalatable plants have developed to the detriment of the pastures.

The virus disease myxomatosis has recently proved fatal to millions of rabbits. Pathologists expect the virus and the rabbits to reach a dynamic balance, with the population of the latter at a less destructive level. It is hoped the virus will not attack other mammalian hosts.

Of the carnivores, the Dingo (*Canis familiaris dingo*) was almost certainly introduced by early aborigines or Malayans. The native Tasmanian Wolf (*Thylacinus cynocephalus*) and the Tasmanian Devil (*Sarcophilus harrisii*) apparently were exterminated from the Australian mainland by competition with Dingos. Interbreeding of the latter with domestic dogs is increasingly common and has already eliminated "pure" Dingos from the more settled areas (Troughton, 1947).

The Red Fox (*Vulpes v. crucigera*) was introduced to Victoria from England in the 1870s for sporting purposes (Jones, 1925). It spread rapidly across the continent, but slowed to a stand-still in the last twenty years. It appears to be absent in the most northern part of the Northern Territory and on the Cape York Peninsula, and is still sparse in the Kimberley Division of Western Australia. Calaby (*in litt.*)

states that the fox's northern limit is beyond that of the rabbit. Foxes prey on most native mammals except the larger kangaroos, and they chase even these until the young ones fall out of the pouch (Stead, 1928).

Ferrets, stoats and weasels (*Mustela* spp.) were brought to Australia in large numbers to prey on rabbits, but proved to be extremely destructive to native birds and smaller mammals. No information was obtained regarding their present status.

The American Gray Squirrel (*Sciurus carolinensis*) occurs in only a few parks within the city of Ballarat, Victoria. These specimens are said to be descended from a single pair liberated about fifteen years ago. This species is also present in the city of Melbourne (Barrett, 1934).

The Indian Palm Squirrel (*Funambulus palmarum*) has become established near the Taronga Park Zoo in Sydney as well as near a local zoo at South Perth (W.A.). These populations represent escapees from the zoos, not deliberate releases.

The European Hare (*Lepus europaeus occidentalis*) was introduced in the 1870s from England to various sites in Victoria for sporting purposes. It is now well distributed over Victoria, New South Wales, parts of southern Queensland and South Australia. It seems not to present any great problem. Apparently it is not affected by myxomatosis.

Fallow Deer were first introduced into the Australian region by Captains Dumaresque and Kemp in 1829. Other species have since been introduced into Victoria (Bentley, 1954). Deer also occur in New South Wales, Queensland and Western Australia.

No less than seventeen different forms of deer were imported by the Victorian Acclimatization Society to their grounds at Royal Park from the 1840s to 1890. Those known to have been liberated in the wild are listed in Table 4. The Roe Deer failed to survive. Others which were introduced, but of which there is no record of their liberation, include the Luzon Sambar, the Moluccan Rusa, the Mule Deer, Chinese Water Deer and Musk Deer. According to offi-

TABLE 4: MAMMALS INTRODUCED INTO AUSTRALIA

Common Name	Scientific Name	Year(s) of Liberation	Country or Place of Origin	Country or Place of Introduction	Reason for Introduction
A: *Successful introductions:*					
European Rabbit	*Oryctolagus cuniculus*	1788	England?	Several states	Hunting
European Hare	*Lepus europaeus*	1870s	England	Victoria	Hunting
Dingo	*Canis dingo*	?	?	?	
European Red Fox	*Vulpes vulpes crucigera*	1870s	England	Victoria	Hunting
European Red Deer	*Cervus elaphus*	1870s	. . .	Several states	Hunting
Sambar Deer	*Cervus unicolor*	1860s	?	Victoria	Hunting
Hog Deer	*Axis porcinus*	1866	?	Victoria	Hunting
Fallow Deer	*Dama dama*	1840s and later	England	Several states	Hunting
B: *Partly successful, success unknown, or unsuccessful introductions:*					
Indian Palm Squirrel	*Funambulus palmarum*	?	?	N.S.W., W.A.	Escaped from zoos
Ferret	*Mustela putorius furo*	?	?	?	Rabbit control
Stoat	*Mustela erminea*	?	?	?	Rabbit control
Weasel	*Mustela* sp.	?	?	?	Rabbit control
Axis Deer	*Axis axis*	1860-1870	?	Victoria	Hunting
Barasingha Deer	*Cervus duvauceli*	1871-1885	?	Victoria	Hunting
Rusa Deer	*Cervus timorensis*	1890	Indonesia	Victoria	Hunting
Sika Deer	*Cervus nippon nippon* and *C. n. taiouanus*	1890 1850s	?	Tasmania	Hunting Hunting
Roe Deer	*Capreolus capreolus*	?	?	Victoria	Hunting

cial records from about 1884, several species of deer were introduced into the National Park, N.S.W. (Troughton, *in litt.*).

Most deer have failed to become established in the wild. In Victoria, the most common deer at present are the Sambar and the Hog Deer. In areas where Red and Fallow Deer do occur, they are not common. Little information is available on the browsing pressure exerted by deer; in localized areas, destruction of farmers' crops has been reported.

Sambar Deer (*Cervus unicolor*), first liberated in 1860, inhabit the hills northeast of Melbourne, and also West Gippsland. The northern and eastern limits of their range are uncertain, but they seem to persist despite considerable hunting pressure. On French Island, a population of Sambar traces back to a number that swam from the mainland in the early 1900s. The species is present in the Grampians and about Mount Cole in western Victoria. The National Park Guide of New South Wales, for 1893, states that Sambar were received via New Caledonia, but there is no indication of their ultimate survival.

Hog Deer (*Axis porcinus*) occur in the coastal areas of Gippsland in eastern Victoria, as far as the region between Nowa and Orbost. A herd is rumored to be present on the Murray River.

Red Deer (*Cervus elaphus*) occur in Victoria, New South Wales, Queensland and Western Australia. The Werribee herd in Victoria developed from six animals of Windsor Park blood imported in 1860. Stock from this herd was distributed throughout Australia and New Zealand. Another herd, introduced about the same time and owned by the Melbourne Hunt, was bred from Windsor Park and Knowsley Park stock; it contributed to the present Victoria population. In Western Victoria, Red Deer are reported from the timbered ranges about twenty miles south of Ballarat, west to Ararat, in the Wartook and Victoria valleys of the Grampians, and possibly in the Otway Ranges. In eastern Victoria, these deer are occasionally taken near Warburton and Gembrook.

Red Deer were liberated near Aston in New South Wales about 1918 and appear to have extended down the Bemm and Brodribb Rivers in Victoria (Bentley, 1954). They presumably also occur in the timbered hills along the Brisbane and Mary Rivers of Queensland. The New South Wales official National Park Guide, for 1893, refers to a donation of five Red Deer in November, 1886 (Troughton, *in litt.*). Their progeny appear to survive. Red Deer have been in the North Dandalup-Pinjarry area, south of Perth, for about fifty years, and seem to be barely holding their own (Calaby, *in litt.*).

Fallow Deer (*Dama dama*) were introduced into Tasmania in 1829 and now represent the bulk of the deer population, although covering less than one-twentieth of the island (H. A. Cox, *in litt.*). Some of these were later shipped to Melbourne and elsewhere. Wild herds were mentioned in the ranges northwest of Bacchus Marsh, Victoria, after 1810. They are now found near Casterton, on the Murray River flats near Wodonga, in the Healesville-Norbethong area and in west Gippsland and the Dandenong Ranges. Hunting has greatly reduced the populaton in several places. In the Glen Innes district (N.S.W.), seven individuals gave rise to a herd of 1,000 by 1939; they proved very destructive, and shooting parties reduced the population to about 200. Much the same history took place in the National Park after 1884 (Troughton, *in litt.*).

Axis Deer (*Axis axis*) were liberated at Bunyip and Wilson's Promontory between 1860 and 1870, but now occur in Victoria only in the Grampians. Some were also liberated in Tasmania about 1834 (Cox, *in litt.*).

Barasingha (*Cervus duvaucelli*) were liberated in Victoria late in the Nineteenth Century and before World War I. A few seem to persist in the Mirboo North area, and possibly elsewhere in remote sections.

Rusa Deer (*Cervus timoriensis*) were released in 1890 from the Victorian Acclimatization Society's grounds at Gembrook, and were flourishing in several places in 1900. They are now occasionally shot in Gippsland.

Japanese Sika Deer (*Cervus n. nippon*) were imported from 1868 to 1887 by the Victorian Acclimatization Society, as were a number of Formosan Sika Deer. A number were liberated at Gembrook between 1887 and 1900. They have been reported on Wilson's Promontory.

Africa:

It is regrettable that no definite information could be collected regarding introduced mammals in most of northern and central Africa. Ellerman & Morrison-Scott (1951) speak of Fallow Deer in North Africa. Other possible introductions have gone unrecorded; various individuals questioned about this matter were unable to provide the requested data.

In Tanganyika, the Pemba and Zanzibar Islands are inhabited by two introduced forms: the Thick-tailed Shrew (*Suncus caerulaeus*) and the Rasse (*Viverricula indica rasse*). The Indian Mongoose (*Herpestes auropunctatus*) has been introduced on Mafia Island (G. A. Swynnerton, *in litt.*).

Only three mammals are known as exotics in South Africa: the European Rabbit, American Gray Squirrel and Fallow Deer. None of these has spread very widely.

The European Rabbit (*Oryctolagus cuniculus*) appears to be the only introduced mammal in South Africa which potentially might become a widespread, serious pest. Fortunately, it is now restricted to Robben Island, an islet in Table Bay near Capetown. As early as 1656, rabbits were sent there by Van Riebeeck to provide food for vessels on their way to the East. These lagomorphs are stunted, and have become a pest by nearly eliminating all plants except inedible species. Consequently, the vegetation of the island is now characterized by its great uniformity (Adamson, 1934). Some years ago an attempt was made to exterminate the rabbits by digging them out, but this failed.

The American Gray Squirrel (*Sciurus carolinensis*) was imported into Capetown by Cecil John Rhodes, probably early in the present century. It was intended to fill a "vacant habitat," namely oak forests (also exotics), but seems to prefer the neighboring orchards (Bigalke, 1937a). A few pairs liberated on an estate on the eastern slopes of Table Mountain increased to occupy an area of land within forty miles of Capetown; this spread of range is well documented by Davis (1950). The species is still expanding its range, and seems likely to continue as afforestation proceeds and the pine plantations mature. This squirrel has become a nuisance to fruit growers, and was placed on the vermin list from 1918 to 1922, when rewards were paid for no less than 11,188 specimens. Destruction of seed has become a serious problem in some plantations. The chief factor limiting the spread of Gray Squirrels is the absence of tall seed-bearing trees; it therefore seems unlikely that they will extend much farther in Cape Province. The groves of oak and stone pine (*Pinus pinea*) in the western Cape satisfy their requirements. Although Gray Squirrels prey on small birds, they do not appear to affect the mammalian fauna (Davis, 1950).

The Fallow Deer (*Dama dama*) was introduced on the lands of the Vereeniging Estates Ltd. until about 1914. A nucleus herd was set free on a well-wooded area of some 3,500 acres, and the population has now increased to approximately 50 individuals. Fallow Deer also occur on two other estates (Bigalke, 1937b.)

Oceanic Islands:

Particular islands and island groups are discussed separately because they are inhabited by specialized faunas which, as a result of virtual freedom from predation, have developed few defense mechanisms and in general are easy prey to aggressive introduced mammals. The environmental resistance encountered by exotics on islands is usually much less than in their countries of origin because of the availability of considerable forage as well as limited competition with native species.

New Zealand, the Caribbean Islands and Hawaii will be discussed separately. On the Galapagos Islands the introduced mammals which have a harmful effect on the native animals and plants are feral species (cattle, horses, donkeys, pigs, goats) and Black Rats (Lack, 1947). Rabbits (sp.?) have been responsible for a reduction of the native finch on Laysan Island.

New Zealand.–No other island group in the world provides such an interesting example of the havoc which introductions cause among native animals and plants as New Zealand. In no other area of comparable size have such a variety of mammals been introduced. Because of the long separation from other large land areas, a flora and fauna have evolved here which are very different from anything found elsewhere.

A major reason for the introduction of so many exotics was the virtual absence of native mammals, limited to only two species of bats. Maoris introduced a rat (*Rattus exulans*) and a dog before the arrival of white settlers. Since a meatless diet is unattractive to white settlers, Captain Cook and other early explorers took particular pains to import goats and other mammals. Still more exotics were introduced to provide hunting, furs for garments and controls for species overabundant due to lack of predation.

Wodzicki (1950) divides these exotics into two major groups: those which are widely distributed, *e.g.* Red Deer and rabbits, and those whose distribution has remained localized.

Many of the mammals in the first group may be considered serious pests. They have spread rapidly and become widely established by taking advantage of the large supply of available food and by considerable protection during the early stages of acclimatization. In some cases, a species first reached an excessively high population, and then declined to a more stable level after the exploitation of the reserve food. The continued spread of exotics has seriously affected the native flora as well as man's agricultural activities. In an attempt at control, as many as 100,000 deer have been shot in a single year.

With the possible exception of the Weasel, the mustelids and the hedgehog are well established throughout the country. Most of these were liberated for the purpose of controlling other animal pests, but they have had detrimental effects on the native and introduced

birds which considerably outweigh their beneficial activities.

Many mammals in the group of localized distribution have also proved troublesome. Their economic importance varies considerably. Chamois (*Rupicapra rupicapra*) and Tahr (*Hemitragus jemlahicus*) are dispersed over areas of many hundreds of square miles, while wallabies and several kinds of deer are restricted to relatively small areas.

When first introduced, each species increased in inverse ratio to the resistance by the environment. In some cases, this full resistance may not have been encountered until the species reached a very high population.

According to Wodzicki (1950), four periods of liberation of exotics may be recognized as follows:

1. From the settlement by the Maoris to the visits of Captain Cook,
2. From the time of Captain Cook's visit until 1840,
3. From the period of regular settlement until about 1900, and
4. The present century.

During the first period, the Polynesian cat and dog and the Maori rat were introduced; these species did no appreciable damage to the native flora and fauna. The second period brings the first intentional introductions of exotics. During the third period, white settlers profoundly changed the nature of the vegetation and also deliberately attempted to acclimatize many new animals.

Wodzicki tabulated exotic mammals according to the country of origin and the number of species that became established. Table 5 is modified from his table. Thirty-six per cent. have failed completely. The native rat and dog succumbed to the competition of their European counterparts. Two species of deer, after a slight initial success, are, so far as is known, either on the decrease (Moose) or completely absent (Mule Deer).

TABLE 5: COUNTRY OF ORIGIN AND TOTAL NUMBER OF MAMMAL SPECIES IN NEW ZEALAND (Modified from Wodzicki, 1950)

Country of Origin	Mammal Species	
	Liberated	Established
Europe and England	20	19
Australia	13	4
Polynesia	2	2
North America	7	4
South America	4	—
Asia	5	5
Africa	2	—
	53	34

Table 6 (modified from Wodzicki) tabulates the successful, partially successful, and unsuccessful introductions into New Zealand, with pertinent details.

Caribbean Islands, West Indies.—Considerable damage has been done to the autochthonous fauna and flora of the Caribbean Islands by introduced mammals. Unfortunately, this damage still continues. The Mongoose may be singled out as exceedingly detrimental; it has probably been instrumental in the complete or nearly complete extirpation of several species of mammals and birds. Many members of the indigenous fauna are continually falling prey to such introduced mammals as cats, dogs, monkeys and opossums. Table 7 lists the known introduced mammals of the Caribbean area. Many exotics introduced during the early days of settlement are unrecorded.

The Mongoose (*Herpestes auropunctatus*), the most destructive exotic animal in the Caribbean area, was brought from India to Trinidad in 1870 and to Jamaica in 1872, for the purpose of controlling introduced rats that were destructive in the sugar cane fields (Westermann, 1953). In later years the Mongoose was introduced in the West Indies. Its introduction on Martinique and St. Lucia was intended to reduce the numbers of the poisonous Fer-de-lance (*Bothrops atrox*), but this met with only partial success (Lewis, 1953). The Mongoose soon became well established and spread extensively; it now occurs on most large and moderately large islands of the Caribbean, but is absent on most of the smaller islets, which therefore serve as useful refuges for species decimated elsewhere.

The Mongoose multiplied rapidly in most places. The four males and five females released on Jamaica increased so quickly, and attacked the rats with such ardor, that in 1882 it was estimated they had saved the planters nearly 45,000 pounds annually. But as soon as the rats were appreciably reduced in numbers, the Mongoose began preying upon native mammals and birds that feed or nest on or near the ground, as well as on such small, harmless creatures as terrestrial snakes, lizards, toads and other amhibians, and land crabs. Eggs of birds and reptiles are also eaten. This havoc has greatly reduced the indigenous fauna and has all but exterminated several species of mammals, birds and reptiles. The killing of small domestic animals has caused serious economic repercussions. Thus, within twenty years after its introduction, the Mongoose had come to be regarded on several islands as the worst of all pests (Westermann, 1953). Furthermore, it has recently been

TABLE 6: INTRODUCTIONS INTO NEW ZEALAND
(Modified from Wodzicki, 1950)

Common Name	Scientific Name	Year(s) of Liberation	Country of Origin	Reason for Introduction
A: *Successful introductions:*				
Brush-tail Opossum	*Trichosurus vulpecula*	1858	Australia	Utility
Scrub Wallaby	*Thylogale* sp.	1870	Australia	Sport and fur
Swamp Wallaby	*Wallabia ualabatus*	1870	Australia	Sport and fur
Black-striped Wallaby	*Wallabia dorsalis*	1870	Australia	Sport and fur
Dama Pademelon	*Thylogale eugenii*	1870	Australia	Sport and fur
Brush-tailed Rock Wallaby	*Petrogale penicillata*	1870	Australia	Sport and fur
Wallaby	Species unknown	1903	Australia	Sport and fur
Hedgehog	*Erinaceus europaeus*	1885	England	"Escapees"
Stoat, Ermine	*Mustela erminea*	1885	England	"Natural enemies" of rabbit
Ferret	*Mustela putorius furo*	1886	England	"Natural enemies" of rabbit
Weasel	*Mustela nivalis*	1885	England	"Natural enemies" of rabbit
European Rabbit	*Oryctolagus cuniculus*	Before 1838	England	Utility
Hare	*Lepus europaeus*	1867	England	Sport
Himalayan Tahr	*Hemitragus jemlahicus*	1904	Asia	Sport
Chamois	*Rupicapra rupicapra*	1889	Austria	Sport
Red Deer	*Cervus elaphus*	1851	England	Sport
Axis Deer	*Axis axis*	1867	India	Sport
Sambar Deer	*Cervus unicolor*	1875	India	Sport
Wapiti	*Cervus canadensis*	1870	Canada	Sport
Japanese Deer	*Cervus nippon*	1885	Manchuria	Sport
Fallow Deer	*Dama dama*	1864	England	Sport
White-tailed Deer	*Odocoileus virginianus*	1901	America	Sport
Moose	*Alces americanus*	1900	Canada	Sport

Common Name	Scientific Name	Year(s) of Liberation	Country of Origin	Reason for Introduction	Reason for Failure
B: *Unsuccessful introductions:*					
Marsupial Cat	*Dasyurus* sp.	1868	Australia	?	Only 2 introduced
Short-faced Bandicoot	*Isoodon* sp.	1873	Australia	?	...
Ring-tailed Opossum	*Pseudocheirus peregrinus*	1867	Australia	Utility	Only 2 introduced
Kangaroo	*Macropus* sp.	1868	Australia	Sport	Only 6 introduced
Roan Wallaroo	*Osphranter erubescens*	1860-1870	Australia	Sport	...
Long-nosed Kangaroo	*Potorous tridactylus*	1867	Australia	?	...
Raccoon	*Procyon lotor*	about 1905	America	Escapees	Only 2 introduced
Chipmunk	*Tamias striatus*	1906	America	...	Only 2 introduced
California Ground Squirrel	*Citellus* ?	1906	America	...	Only 2 introduced
Guinea Pig	*Cavia porcellus*	1869	America	Stowaways	...
Bharal or Blue Sheep	*Pseudois nayaur*	1909	Asia	Sport	Only 3 introduced
Gnu	*Connochaetes gnou*	1870	S. Africa	?	Only 1 introduced
South American Deer	*Cariacus chilensis* (=*Hippocamelus bisulcus?*)	1870	S. America	Sport	Only 1 introduced
Alpaca	*Lama glama huanacus*	1878	S. America	Sport	Only 3 introduced
Zebra	*Equus zebra*	1870	S. Africa	?	Only 2 introduced
Mule Deer	*Odocoileus hemionus*	1905	America	Sport	...

implicated as a reservoir of the virus of canine rabies (Seaman, 1952).

Two species of monkeys have been introduced into the Caribbean area. The Green Monkey (*Cercopithecus aethiops sabaeus*) from West Africa was introduced on Barbados between 1673 and 1750; in 1903 it was found at only a few points where woodland persisted; it is still present today, in small numbers. The species was also introduced on St. Kitts and Nevis where it is still rather common. These monkeys prey on the eggs and young of birds, and are believed to have exterminated the St. Kitts Bullfinch (*Loxigilla portoricensis grandis*). The Mona Monkey (*Cercopithecus mona*), now present on Grenada, is native to the Cameroons and adjacent parts of West Africa and was possibly introduced by slave traders (Westermann, 1953).

The Opossum (*Didelphis marsupialis insularis*) was introduced from Trinidad into Grenada, the larger Grenadines, St. Vincent, St. Lucia and Dominica, where it has apparently played a role in the nearly complete disappearance of the Ground Dove (*Scothrygon mystacea*) (Barbour, 1930). It is uncertain whether another species of opossum (*Marmosa mitis chapmani*), found on Grenada and some of the Grenadines, is native to these islands.

On Great Bahama Island one pair of Raccoons (*Procyon lotor*) from the Florida mainland were released about 1932; they are now considered a nuisance over the entire island (Sherman, 1954). It is conjectural whether or not another species of Raccoon (*Procyon maynardi*) was imported by man to New Providence Island in the Bahamas. *Procyon minor* of Guadeloupe, and *Procyon* sp. of Barbados, may also be exotics (Allen, 1911).

Several species of deer have been introduced on various Caribbean Islands. Whitetail Deer (*Odocoileus virginianus*) were brought to Cuba from Mexico and/or the southern United States, presumably about 1850. They formerly were

TABLE 7: SUCCESSFUL INTRODUCTIONS ON SELECTED ISLAND GROUPS*

Common Name	Scientific Name	Year(s) of Liberation	Country or Place of		Reason for Introduction
			Origin	Introduction	
Opossum	*Didelphis marsupialis insularis*	?	Trinidad	Caribbean Is.	?
Mona Monkey	*Cercopithecus mona*	?	West Africa	Grenada	Pets
Green Monkey	*Cercopithecus aethiops sabaeus*	1673-1750	West Africa	Caribbean Is.	Pets
European Hare	*Lepus europaeus occidentalis*	?	Europe	Caribbean Is.	Hunting
European Hare	*Lepus europaeus*	?	Russia	Islets off Oahu	Hunting
European Rabbit	*Oryctolagus cuniculus*	?	Europe	Caribbean Is.	Hunting
Black-naped Rabbit	*Sylvilagus nigronuchalis*	?	Venezuela?	Curaçao, Aruba	?
Agouti	*Dasyprocta aguti*	Before 1852	Brazil?	St. Thomas Is.	?
Red Agouti	*Dasyprocta punctata*?	1890s	C. America	Cayman Is.	?
Mongoose	*Herpestes a. auropunctatus*	1870 and later	India	Caribbean Is.	Rat control
Mongoose	*Herpestes a. auropunctatus*	1883	Jamaica	Hawaii	Rat control
Axis Deer	*Axis axis*	?	?	Hawaii	Hunting
Mouflon	*Ovis musimon*	1954	Europe	Hawaii	Hunting
White-tailed Deer	*Odocoileus virginianus*	1850s	Mexico, U.S.A.	Cuba and other islands	Hunting
White-tailed Deer	*Odocoileus virginianus curassavicus*	?	Colombia	Curaçao	Hunting
Sambar Deer†	*Cervus unicolor*	During Spanish occupation	Philippine Is.	Guam, Rota	Hunting

* Except New Zealand.
† R. H. Baker (1946).

more abundant, but have disappeared from many areas because of deforestation. A South American race (*O. v. curassavicus*) is thought to have been imported from Colombia to Curaçao. Deer of this or other genera have reached the Dominican Republic, Jamaica, U. S. Virgin Islands, Barbuda, Dominica, Grenada and possibly other islands (Westermann, 1953).

The European Hare (*Lepus europaeus*) and the European Rabbit (*Oryctolagus cuniculus*) have been reported introduced into Barbados, one of the Grenadines, and Guadeloupe (Allen, 1911): Another rabbit (*Sylvilagus nigronuchalis*) is supposed to have been introduced into Curaçao and Aruba.

Agoutis have been introduced into St. Thomas and the Cayman Islands. The species of St. Thomas is *Dasyprocta aguti*, probably obtained from Brazil prior to 1852 (Miller, 1918). The Cayman animal is a Red Agouti derived from Central America in the 1890s or earlier. It has rendered certain areas virtually useless for cultivation, and at present the Government pays a bounty of nine pence per head for its destruction (Swabey & Lewis, 1946).

Hedgehogs may have been introduced from Africa to Porto Rico before 1877, for the type specimen of *Erinaceus krugi* Peters (=*E. algirus caniculus*) was killed in Mayaguez, Porto Rico. Seemingly the species did not survive, for there are no recent records of them on this island.

Hawaii.—The Hawaiian Islands have only one native mammal, the Hawaiian Hoary Bat (*Lasiurus*). Introduced mammals have therefore exerted pressure mainly on the native birds, and there is little doubt that they have contributed to the decline of several species of land and sea birds. Depredations by certain mammals have been more serious in regard to eggs and young than to adult birds. It is likely that certain species of plants which served either as cover or as food, or as a link in the food chain of the nectar-feeding and insect-feeding birds, were destroyed or sufficiently reduced by introduced forms to contribute to the decline of certain native bird species (Schwartz, *in litt.*).

Table 7 includes the known introduced mammals of Hawaii.

Axis Deer (*Axis axis*) occur in limited numbers, but in dense concentrations, on Molokai, Oahu and Lanai. They cause damage by browsing where native flora still exists. Some legal hunting is permitted, but since the species is found on private land, no regulation of herds is attempted (Schwartz, *in litt.*).

A hare, believed to be of Russian origin (species unknown), is found on two small uninhabited islets consisting of only a few acres each, off Oahu. The animal is not abundant (Schwartz, *in litt.*).

A herd of Mouflon (*Ovis musimon*) was liberated on Lanai during the summer of 1954, according to a report of the Committee on Fauna Conservation of the Conservation Council for Hawaii (1955).

The Mongoose (*Herpestes auropunctatus*) was introduced from Jamaica in 1883. It now occurs on all major islands except Kanai, Lanai and Niihau. It is abundant and the heaviest populations are found near sea level. The merits of the Mongoose in the control of rodents are doubtful; the sugar producers have their own regular program of rat control. In the past, futile attempts have been made to control the animals. Territorial laws prohibit transporting them between any of the islands of the group. The Mongoose has probably contributed to the destruction of some ground-nesting sea birds, as well as of the Nene Goose, Hawaiian Owl, Hawaiian Duck, Hawaiian Coot and Hawaiian Gallinule (Schwartz, *in litt.*).

Introduced Rats, Mice and Shrews

The introduced Old World murids are among the most notorious of mammalian pests. The history of their spread (Silver, 1927) has been recounted so frequently that it need not be detailed here. They affect man's economy by eating and contaminating food, and they also carry epidemic diseases and parasites. As stowaways in ships, two species of rats and the House Mouse have been involuntarily spread by man throughout most of the world, including many scattered islands. These exotics are usually restricted to human habitations and their environs.

The rats concerned are the Norway or Brown Rat (*Rattus norvegicus*) and the Black or Roof Rat (*Rattus rattus*), several subspecies of which have been involved. The Norway Rat has by far the wider distribution and the greater abundance. It occurs in almost all coastal cities of the world, but also has spread widely inland. The Black Rat is generally considered to be less aggressive than the Norway Rat, and where the two compete it is often forced into the less desirable habitats. The Black Rat came to Europe in early times from Asia, probably on ships of the Crusaders sometime after 1191, and by the Middle Ages it had spread over most of the Old World. The Norway Rat arrived in Europe early in the Eighteenth Century, crossing the Volga in great numbers in 1727, reaching East Prussia in 1750 and Spain in 1800. The Black Rat and the House Mouse arrived in North America very soon after the first European visitors. The Alexandrine Rat (*Rattus r. alexandrinus*) is restricted to rather limited

areas on all continents except Australia. *Rattus r. frugivorous* has been recognized in recent years as part of the population in the United States.

Introduced rats are blamed for the destruction of small insectivores (*Nesophontes*) and native Rice Rats and Spiny Rats on the Caribbean Islands (Westermann, 1953). In Australia, the native rats are normally slower breeders than the two introduced species and have consequently been displaced in many places by these exotics (Troughton, 1947).

The House Mouse (*Mus musculus*), originating in Asia, has established itself not only around human habitations but also in the field, especially in the more moderate climates. In Africa and Australia it is now present over large areas, even very far from settlements. On the latter continent, as well as in North America, it is subject to irregular irruptions and during peaks of population it does tremendous damage to the vegetation. Introduced House Mice have developed new subspecies in several parts of the world. On the Faroe Islands, for example, four distinct subspecies exist today (Bourlière, 1954).

The House Shrew (*Suncus murinus*) has been spread by man throughout most of the southeastern Asian islands.

Feral Mammals

Feral mammals have been transplanted by man as domestic stock or as pets, and have since escaped or been purposely released and then "reverted to nature" to various degrees. Although feral mammals may be of considerable biological and economic importance, they have received little attention from zoologists.

Domestic horses, cattle, sheep, goats, pigs, dogs and cats are now almost cosmopolitan in distribution, and also occur widely in the wild state. Many less known feral mammals such as buffaloes and camels populate certain parts of the world.

Feral ungulates provide meat in considerable quantities, and sport for the hunter. Some are considered harmful because of damage to the native fauna and flora and because they may harbor diseases affecting domestic stock.

The domestic goat (*Capra prisca*) undoubtedly has been the most destructive of feral mammals to native vegetation, particularly as it travels over all types of terrain and consumes all kinds of browse and herbaceous material. Feral goats occur on all continents, even in such places as the Scottish Highlands. In Australia they are well established in the dry interior (Calaby, *in litt.*). They are a serious problem on many islands, such as New Zealand (Thomson, 1922), Hawaii and several of the Caribbean islands. A typical picture is that presented by Wallace (1880) of the island of St. Helena: "At the time of its discovery, about the beginning of the sixteenth century, it is said to have been covered by dense forest; to-day it is described as a comparatively barren, rocky desert. This change has been brought about by goats first introduced by the Portuguese in 1513, and which multiplied so fast that in seventy-five years they existed by thousands." Heavy browsing destroyed the vegetation, followed by erosion of the soil by tropical rains. The story is similar on Guadalupe Island, in the Pacific, where goats were released by Russians in the Eighteenth Century. Many species of plants and animals, particularly birds, apparently disappeared forever.

Feral sheep (*Ovis aries*) cause considerable damage to the forests on the Hawaiian Islands. Elsewhere they are not considered a menace by agriculturalists.

Feral pigs (*Sus scrofa*) are widespread throughout the world. In Australia, where they occur in almost every state, they are a problem for graziers (Pullar, 1953). In Hawaii they are sometimes a serious threat to wildlife, including the nearly extinct Hawaiian Goose (Schwartz, *in litt.*; Bryan, 1937). Man imported them to most of the South Sea islands and to the Galapagos Islands. In parts of New Zealand they are very destructive to vegetation. The pigs in the eastern part of the Indonesian Archipelago are presumably descendants of domestic stock, but in some places they may have hybridized with wild species. It is probable that the pigs on New Guinea are direct descendants of domestic stock.

Feral horses (*Equus caballus*) still occur in Australia, New Zealand, North and South America and Asia, and where they become too plentiful they compete critically for food with domestic stock and native wildlife. Feral donkeys (*Equus asinus*) are present in northwestern Australia and the Northern Territory (Calaby, *in litt.*). Some "burros" also are present in herds in places on the southwestern deserts of the United States (Anon., 1952b; Davis, 1953).

Feral cattle (*Bos taurus*) survive in fair numbers chiefly in Australia, where they are restricted to parts of Western Australia, the Northern Territory and western Queensland. They also are found in some numbers in New Zealand and in parts of the western United States (Linger, 1943). Indian Water Buffaloes (*Bubalus bubalis*) occur in large herds in certain valleys of northern Australia (Calaby, *in litt.*). Feral Water Buffaloes also occupy many

countries in southeastern Asia and the island of Marajo in Brazil.

Feral Camels (*Camelus dromedarius*) are now found in large numbers in the more arid parts of Australia (Calaby, *in litt.*) and of central Asia, and in small numbers in the Kalahari Desert of southern Africa (Cahalane, *in litt.*). Several attempts, prior to 1860, to establish them in Texas, Cuba, Jamaica and South America were unsuccessful (Goodwin, 1925).

Llamas (*Lama glama*) may have been introduced in Mexico as beasts of burden in the Sixteenth Century. None are present there today.

Reindeer (*Rangifer tarandus*), introduced into Alaska and Canada, have hybridized to some extent with the native Caribou (*R. arcticus*), with resultant genetic changes in each. These Reindeer have done considerable localized damage to Caribou range by overgrazing lichens (Cahalane, 1950; Hanson, 1952). A recent introduction of Reindeer into Scotland has failed, but the species has been successfully introduced to Iceland. The establishment of Reindeer in Tierra de los Estados is reported by Cabrera & Yepes (1940), but details of the results are lacking.

Among the feral carnivores, cats and dogs are the most destructive species. Both revert to the wild readily and, being efficient predators, they may do much damage to wildlife. Dogs and cats are responsible for the disappearance of several forms, particularly in the Caribbean area, in Australia and on small islands.

Introduction of Diseases and Parasites

A consequence of animal introductions generally not fully appreciated is the importation of diseases and parasites of which the exotics are hosts. Most diseases are more dangerous to a previously unexposed population, since no immunities have been developed. Introduced diseases may easily become established in native species, and may prove impossible to eradicate.

Two epizootic diseases, rinderpest and foot-and-mouth disease, are particularly destructive after introduction. Rinderpest, or cattle plague, introduced from Asia to Africa, killed many ungulates. The Cape Buffalo (*Syncerus caffer*), common before the disease was introduced, was almost extirpated in the first outbreak. Although methods of artificially immunizing domestic stock are available, these cannot be applied to wild game.

Foot-and-mouth disease, endemic to Eurasia, has been introduced twice with domestic stock to North America, but fortunately was extinguished in the United States and Canada. It is, however, present in Africa, Mexico and South America, where thousands of wild ungulates have been killed in a futile attempt to combat it.

There are few data on the introduced parasites of exotic mammals and their possible influences on native hosts. Two pertinent papers dealing with the endoparasites of the European Rabbit in New Zealand (Bull, 1953) and of the Muskrat in Great Britain (Warwick, 1936) have come to our attention. These papers raise several interesting points, on which further information is desirable.

First, they indicate that parasites do get introduced, and sometimes several species at once. For example, of five nematodes and two cestode species found in the rabbits of New Zealand, three of the nematodes and both cestodes also are found among rabbits in Wales. The other two nematodes perhaps were acquired in New Zealand. The rabbit is one of the intermediate hosts for the two cestodes, which are carried in vesicles within the body, in the larval stage only. Another cestode, *Cittotaenia* sp., for which the rabbit is the definitive host of the adult stage, apparently is absent from rabbits in New Zealand, as well as in Australia. Possibly it failed to survive the long voyage from England (and the periods of confinement before and after the voyage) because of the absence of its only known intermediate host, a free-living oribatid mite.

At least two parasites, a cestode and a trematode, were introduced with the Muskrat hosts from North America to Great Britain. Two others might also have been introduced, had they not already been present in Great Britain. One other parasite was apparently acquired from the native fauna.

Second, it is possible for introduced parasites to be transferred to closely related or associated species of hosts. In North America, parasites of the Muskrat often are shared with the Meadow Vole (*Microtus pennsylvanicus*). Such an exchange might take place between introduced Muskrats in Europe and the Water Vole (*Arvicola terrestris*) or other species of voles. Table 8

Table 8: Parasites Shared by the Muskrat and the Meadow Vole

	Species of Parasites in the Muskrat*	Species also Present in the Meadow Vole
Trematodes	30	4
Cestodes	10	4
Nematodes	9	2

* Data summarized from various reports.

lists the number of species of helminth parasites in North American Muskrats, and the number of those species which have also been found in the Meadow Vole.

Third, the more complicated the life cycle of the introduced parasite, the less likely is its chance for survival. Trematodes with a life history involving two or more intermediate hosts may not find suitable hosts in a new environment. Nematodes may be introduced with relative ease because many of them are transmitted directly from one final host to another, the intervening stages being free-living. Introduction of cestodes in the larval stages may be fairly easy, but survival depends upon the presence of a suitable final host (a carnivorous bird or mammal) in the new area.

Rausch & Schiller (1954) mention the introduction from Siberia to Bering Island of the larval stage of a possible Siberian cestode, *Echinococcus* sp., with its host the Red-backed Vole; the island foxes became infected with this cestode.

Little information could be secured about the transfer of ectoparasites with mammals. It seems likely that the tick, *Trombicula akamushi,* which harbors the rickettsial disease, scrub typhus, has been spread widely with introduced rats or other rodents. The Indian rat flea, *Xenopsylla cheopis,* which transmits bubonic plague, has also been spread widely with rats on ships into many parts of the world.

Summary

For a variety of reasons, man has seen fit to transport mammals from one part of the world to another. These introduced forms have frequently failed to become established; when establishment did result, the exotics have usually failed to achieve the purpose of the introduction. Sometimes they have become serious economic pests, as well as exerting an unbalancing force on the local biotic equilibrium.

This paper, largely restricted to the problem of deliberately introduced mammals, discusses more than 200 cases of exotic species on different continents and islands.

Certain principles may be deduced from the study of introductions and transplantations of mammals. Some of these principles are described by Dice (1952); some principles and implications are discussed by Pierce (1956).

1. The result of an introduction is unpredictable; both the relative success with which it establishes itself and the amount of disturbance produced in a community through its presence depend upon the newcomer as well as upon the composition of the invaded community. The more specialized a species is, the more difficulty it usually encounters in becoming established, and the less likely it is to become a pest.

2. No exotic mammal is identical in its various requirements with any native member of a community; this results in conflicts and causes numerous readjustments, often detrimental, in the ecologic organization of a community. One result is the reduction or elimination of certain native species. Established exotics may supplant closely related native species, often because they have a higher reproductive potential.

3. When an introduced species differs greatly in habits from existing members of a community, it may produce serious changes in the entire community. Thus goats introduced on certain oceanic islands have caused the virtual annihilation of vegetation and the consequent disappearance of many native forms. Mammals which are apparently harmless in one area may become serious pests in another. For example, the Phalanger is innocuous in Australia, but very harmful in New Zealand.

4. Genetic changes may occur in species after introduction to a new habitat. This is possibly due to the limited quantity of genetic material available when only a few individuals are introduced. For example, Mouflons introduced into Slovakia developed a new race expressed by different color of hair and shape of horns.

5. The transplantation of one form into the existing range of another form of the same species often results in the production of a mixed race, with sometimes serious complications, especially when the introduced form is in some respect less desirable than the native. In Czechoslovakia, for example, two introduced species of goat have interbred with the native Ibex, resulting in poor survival of the hybrids.

6. Some species change their habits in a new environment, often with serious consequences for existing communities and for man. The Raccoon-dog has apparently altered its food habits after introduction into the Caucasus; this is also the case with the American Gray Squirrel in South Africa and with the Formosan Gray-headed Squirrel in Japan.

7. An introduced species which establishes itself successfully seems to pass through two definite phases of population behavior: at first it multiplies rapidly and builds up to a peak population; thereafter it levels off to a point of moderate abundance, or may even become rare. The initial increase may be due to the lack of natural parasites or other controlling factors, which in time develop to again produce a stabilized community, but one with a changed composition.

8. Exotic species which become established as thriving populations usually do so at the expense of one or more native species. There is little evidence to indicate that the total supply of game will be increased by adding a new game species to a habitat already occupied by one with similar requirements; the habitat can support permanently only a certain population. Occasionally "vacant" niches may be occupied by exotics; this may be the case with the European Hare on farm lands in eastern North America, or with the Moose in Newfoundland.

9. The problems of chance introductions and of feral mammals are similar to those of deliberate introductions of wild species.

10. Control of a well-established introduction is extremely difficult. The only known case of the eradication of an introduced mammal which was distributed over a fairly wide range is that of the Muskrat in the British Isles.

11. There is evidence that parasites and diseases of introduced mammals are at least partly transferred with their hosts to new biota.

12. The evidence accumulated in this paper indicates that the introduction of mammals is a hazardous undertaking and that further introductions should be more carefully considered in advance. The introduction of a mammal for the sole purpose of controlling pests is almost certainly doomed to failure. Food habits are rarely so specialized that a mammal will feed entirely on the pest to be controlled. Few mammals introduced for sport have proved eminently successful.

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